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GORDON P. DEWOLF, JR., Editor-in-Chief

Associate Editors

DAVID S. CONANT

LISA A. STANDLEY

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A VEGETATION AND FLORISTIC ANALYSIS OF A CREATED WETLAND IN SOUTHEASTERN NEW HAMPSHIRE

DONALD J. PADGETT AND GARRETT E. CROW

ABSTRACT

The artificial creation of wetlands has become a common means to mitigate the effects of wetland alteration due to development. The establishment of diverse, functional plant communities is a crucial and challenging part of a wetland creation project. This study analyzes plant community structure of a seven year old, artificially created wetland. One hundred and four vascular plant species are documented from the study site including two species listed as rare for New Hampshire and the first state record for an introduced weedy species.

The computer program TWINSPAN used species abundance data to classify the vegetation into seven cover types. The three plant associations of the open water habitat were: *Chara* cover type, *Potamogeton pusillus* cover type, and the *Potamogeton natans* cover type. The four plant associations of the emergent habitat were: *Eleocharis smallii* cover type, *Typha latifolia* cover type, *Juncus effusus-Phalaris arundinacea* cover type, and a *Carex stricta* cover type. Each cover type and associated habitat was described and delineated.

Key Words: floristics, wetlands, wetland mitigation, rare plants

INTRODUCTION

Encompassing such diverse systems as freshwater marshes, swamps, bogs, sloughs, ponds and lakes, rivers and streams, coastal freshwater tidal marshes, and saltmarshes, wetlands collectively constitute one of the most productive biomes on Earth (Good et al., 1978; Mitsch and Gosselink, 1986). Beyond the obvious aquatic productivity and associated food-chain support, wetland ecosystems are vital in performing numerous other ecological functions (Goodwin and Niering, 1974; Burke et al., 1988; Larson, 1988). The rather late recognition of wetland values and functions over the past two decades seems to have been catalyzed by the alarming

rate at which wetlands are being destroyed. Most important, the vital role wetlands play in the overall quality of the environment has finally been recognized and a variety of efforts are being implemented to provide a means for their conservation.

One strategy that has been developed to conserve wetlands is termed wetland mitigation. Wetland mitigation reduces or compensates for the negative impacts on aquatic ecosystems imposed by development by artificially creating or restoring wetland areas (Savage, 1986). Mitigation has become an integral part of wetland protection and conservation policies. Wetland mitigation attempts to restore to an area those functions of a wetland that are impacted or destroyed.

The primary goal of wetland creation or restoration projects typically aims at restoring lost wetland functions. Wetland creation efforts additionally aim at creating an area that is at least the same size as the area lost and the establishment of certain wetland vegetation types (Lowry, 1990; Kruczynski, 1990).

The establishment of hydrophilic vegetation is crucial in wetland mitigation projects if they are to imitate successfully natural wetland ecosystems. Wetland vegetation provides some of the important functions and values inherent in wetlands (Good et al., 1978; Mitsch and Gosselink, 1986) and creates suitable habitats for wildlife (Weller, 1978). The establishment of diverse, functional wetland plant communities is a challenging part of mitigation projects (Padgett and Crow, in press).

The objective of the present study is to provide a detailed vegetation analysis and total floristic inventory of a seven year old, artificially created, freshwater wetland located in southeastern New Hampshire.

Site History

During the winter of 1985–86, the Hospital Corporation of America (HCA) created a freshwater wetland under the Section 404 guidelines of the U.S. Army Corps of Engineers to compensate for the filling of a wetland at the construction site of a new regional hospital in Portsmouth, New Hampshire. The land area designated for the creation of the compensatory wetland was an abandoned gravel pit located approximately 3 miles from the hospital site in the southern end of Portsmouth, NH (Rockingham Co.) (Michener et al., 1986). The size of the mitigation area (ca. 13

acres) was similar to the size of the area lost due to the hospital construction.

Wetland construction began in the fall of 1985 and continued through the winter of 1986. Basins were excavated and graded to form a sinuous configuration of open water pools and marsh areas (Michener et al., 1986). The wetland soils and peat at the new hospital site (impacted wetland) were excavated and transported to the new wetland creation site. This material was stockpiled through the winter and eventually spread as a 6–12″ top dressing over the excavated basins.

The primary strategy to vegetate the newly created basins was to allow for the natural colonization of wetland plants. Therefore there was no direct planting of wetland plant stock. The muck top dressing was expected to serve as a created "seed bank" naturally holding large quantities of plant seeds and vegetative propagules (Michener et al., 1986).

Groundwater is the primary hydrological input into the site. Groundwater flow is westward, discharging into the adjacent forested swamp (Garlo, 1993). However, during the first summer after construction, beavers dammed the small outflow channel. Consequently, the water level was raised approximately two feet above the design elevation.

Site Description

The H.C.A. Portsmouth wetland is a created freshwater wetland consisting of primarily herbaceous aquatic plants. Some tree and shrub areas exist on several upland islands and pool margins. Open water areas form sinuous configurations around these islands. The maximum depth of the open water areas is approximately two meters. The created wetland is surrounded by upland forest communities on the northeastern and southern sides, and a wetland forest community on the northwestern side. A disturbed, open, sandy area with few woody plants surrounds the wetland on the southeast side.

MATERIALS AND METHODS

Vegetation Analysis

Vegetation data were collected during July of 1992. Sampling was done using a systematic sampling method (Mueller-Dombois

and Ellenberg, 1974). Thirteen transects were established across the wetland at 20 meter intervals. A single 0.5 × 0.5 m quadrat was placed at every five meters of transect for a total of 284 sample plots. Trees, shrubs and herbs occurring on the banks and upland sites on the islands throughout the wetland were not included in the sampling.

A visual estimate of percent cover was recorded to estimate abundance. The primary focus of the vegetation analysis was vascular plant species. However, because of their relative abundance *Chara* cf. *vulgaris* and *Ricciocarpus natans,* two non-vascular aquatic plants, were included in the vegetation analysis. Cover was defined as the vertical crown or shoot-area projection per species in relation to the reference area (Mueller-Dombois and Ellenberg, 1974).

The data were analyzed using TWINSPAN (Two-Way Indicator Species Analysis), a fortran classification analysis program. The program first constructs a classification of samples and then based on this classification, constructs a classification of species according to their ecological preferences (Hill, 1979).

TWINSPAN groups the quadrat samples according to the floristic similarity of its members. Using these groups as a basis, species are clustered to form hierarchial dichotomies. There are three ordinations involved in determining a dichotomy: 1) a primary ordination, made by a method of reciprocal averaging; 2) a refined ordination, using differential species determined from the primary ordination; and 3) an indicator ordination, using highly preferential species (Hill, 1979). Corresponding to the Braun-Blanquet cover-abundance scale of 0, 5, 25, 50 and 75 percent (Mueller-Dombois and Ellenberg, 1974), abundance data of TWINSPAN "pseudo-species" were classified at cut levels of 1, 2, 3, 4 and 5 respectively. Ultimately, a two-way table is generated grouping similar quadrat samples across the top and similar species down the left side (Padgett, 1993).

A vegetation map (Figure 2) was prepared based on cover types of quadrats along the 13 transects to give a visual estimate of the pattern of distribution of the seven cover types.

Floristic Study

An inventory of the vascular plants of the site was undertaken during the 1992 field season. Voucher specimens were collected

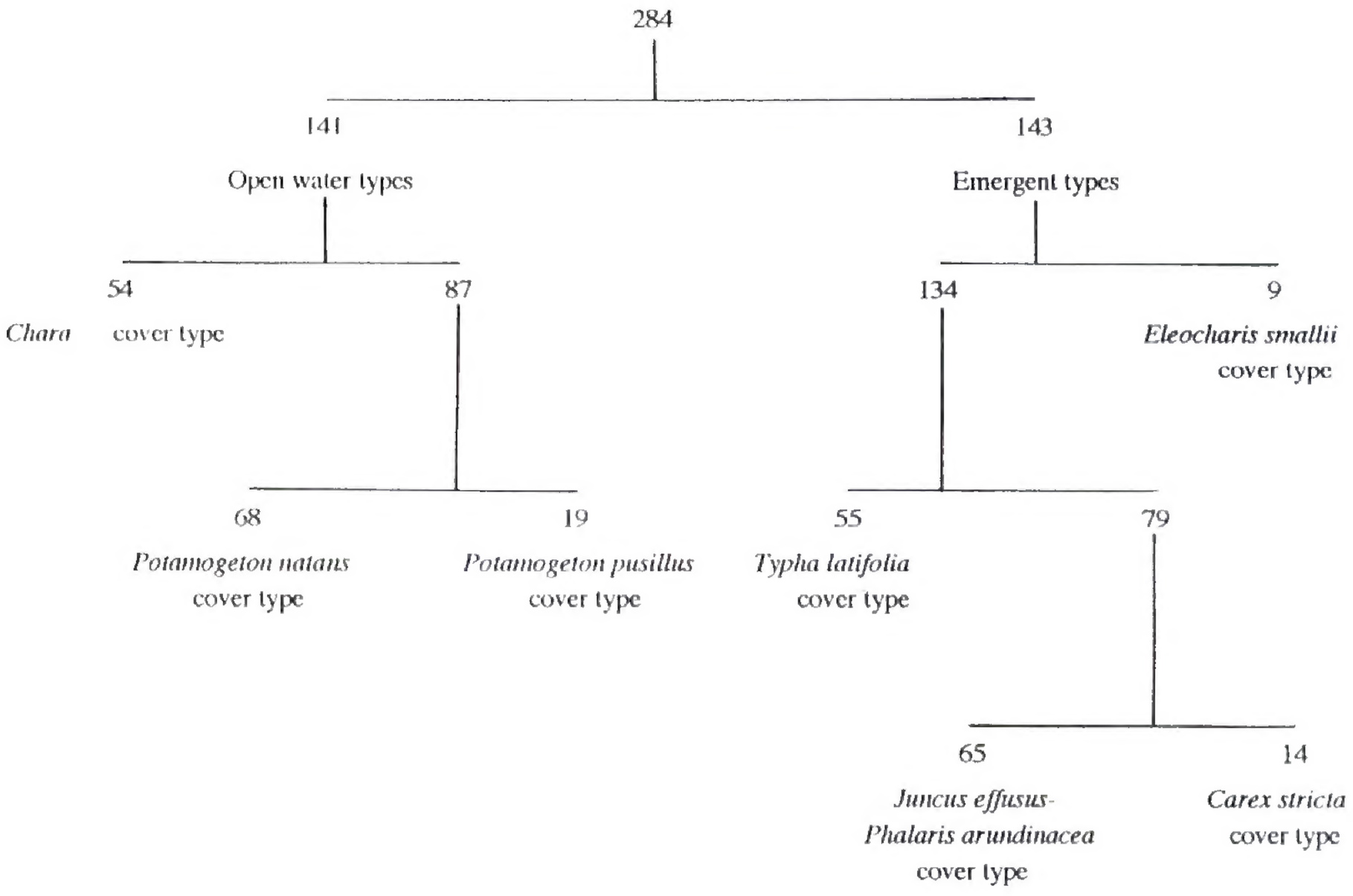

Figure 1. TWINSPAN analysis showing the seven plant cover types classified at four hierarchical levels. Numerals represent the number of quadrats included in each dichotomy.

and deposited in the Hodgdon Herbarium (NHA) at the University of New Hampshire.

Nomenclature follows *Aquatic and Wetland Plants of Northeastern North America* (Crow and Hellquist, in press) and *Manual of Vascular Plants of Northeastern United States and Adjacent Canada* (Gleason and Cronquist, 1991).

RESULTS AND DISCUSSION

The construction of the H.C.A. Portsmouth wetland has created a unique environment, allowing for a natural colonization and emergence of wetland plant species. The various micro-habitats formed by the gradual slopes of the basins and integration of raised islands provide a heterogeneous ecosystem. As a result, concentric vegetation zones have developed according to the ecological affinities of species characteristic of natural wetland systems. The vegetation patterns of the site are typical of those described for inland freshwater wetlands (Mitsch and Gosselink, 1986; Hammer, 1992; Weller, 1978; Curtis, 1959). Generally, for most inland wetlands, sedges (*Carex*) and rushes (*Juncus*) occupy

the wet-meadow areas gradually passing into the shallow water areas colonized by Cattails (*Typha*), Bulrush (*Scirpus*) and Pickerel Weed (*Pontederia cordata*). The deeper, open water areas are colonized by submerged species (*Utricularia*) and floating leaved species (*Potamogeton* and *Nuphar*).

Plant Cover Types

The wetland vegetation was classified using TWINSPAN into seven cover types (Figure 1). Data from 284 quadrats were analyzed and 67 species were clustered at four hierarchical divisions into the seven cover types which could be visually recognized in the field.

The first dichotomy grouped the 284 quadrats into two major groupings, with 141 quadrats representing the open water cover types, and 143 quadrats representing the emergent cover types. At the second level of clustering, 54 quadrats of open water types were distinguished as the *Chara* cover type, with 87 quadrats remaining to be sub-clustered. At the third level 68 quadrats represented the *Potamogeton natans* cover type and 19 quadrats defined the *Potamogeton pusillus* cover type.

TWINSPAN grouped the 143 quadrats in the emergent cover type group into four cover types (Figure 1). At the second level the *Eleocharis smallii* cover type was recognized (9 quadrats). At the third level the *Typha latifolia* cover type was distinguished (55 quadrats), while the *Juncus effusus-Phalaris arundinacea* (65 quadrats) and *Carex stricta* (14 quadrats) cover types were not defined until the fourth level.

The clustering of the quadrats at the first divisional level clearly correlates with the two primary habitats designed for the site creation. The open water cover types occupy the areas where the water is too deep to be colonized by emergent species. Most of the open water areas were vegetated by floating-leaved, free-floating and submerged species. However, some areas remained devoid of vascular plants. For instance, one open pool was heavily colonized by filamentous algae. Although three cover types were recognized as the open water areas, these were not characterized by distinct vegetation zones. Instead these cover types occurred in a mosaic pattern.

The emergent cover types represent the marsh or wet meadow regions designed for the wetland. These areas are defined by a

topographic gradient beginning in the shallow fringe areas of the open pools and extending back into the higher areas of the marsh. Consequently, the emergent cover types are better characterized by zonational patterns when compared to the open water cover types. The emergent cover types are the most floristically diverse areas of the wetland and are characterized by a predominance of emergent species. However, the free-floating *Lemna minor* was found in greater frequencies and abundance within the emergent cover types than in the open water cover areas.

OPEN WATER COVER TYPES

Potamogeton natans Cover Type

The *Potamogeton natans* cover type is the largest plant association of the open water types (Figure 2), defined by the 68 quadrats clustered by TWINSPAN. Of the seventeen species that characterize the community, the floating-leaved *P. natans* is dominant with 35% cover and 90% frequency (Table 1). The submerged *Najas minor* and *Utricularia gibba* are sub-dominants with 11% and 9% covers, respectively, although *U. gibba* has a significantly higher percent frequency. The delicate morphology of *U. gibba* does not allow for high percent coverage.

The cover type is easily discernible by the presence of broad floating leaves of *Potamogeton natans* that form an expansive cover on the surface of the water. This floating-leaf layer was so extensive in certain portions of the wetland, particularly in the northwestern pool, that few open surface water areas were present. Although the cover of *P. natans* was very extensive, the mean percent cover of *P. natans* throughout the entire cover type was only 35%. In areas that were sparsely populated with *P. natans* submerged species, such as *Najas minor, Utricularia gibba* and *P. pusillus,* were frequent.

Chara Cover Type

The *Chara* cover type is one of the larger plant associations of the open water types (Figure 2). The community can be characterized by 15 species, but the macrophytic alga *Chara* cf. *vulgaris* dominates with 81% cover and 98% frequency (Table 2). Plants

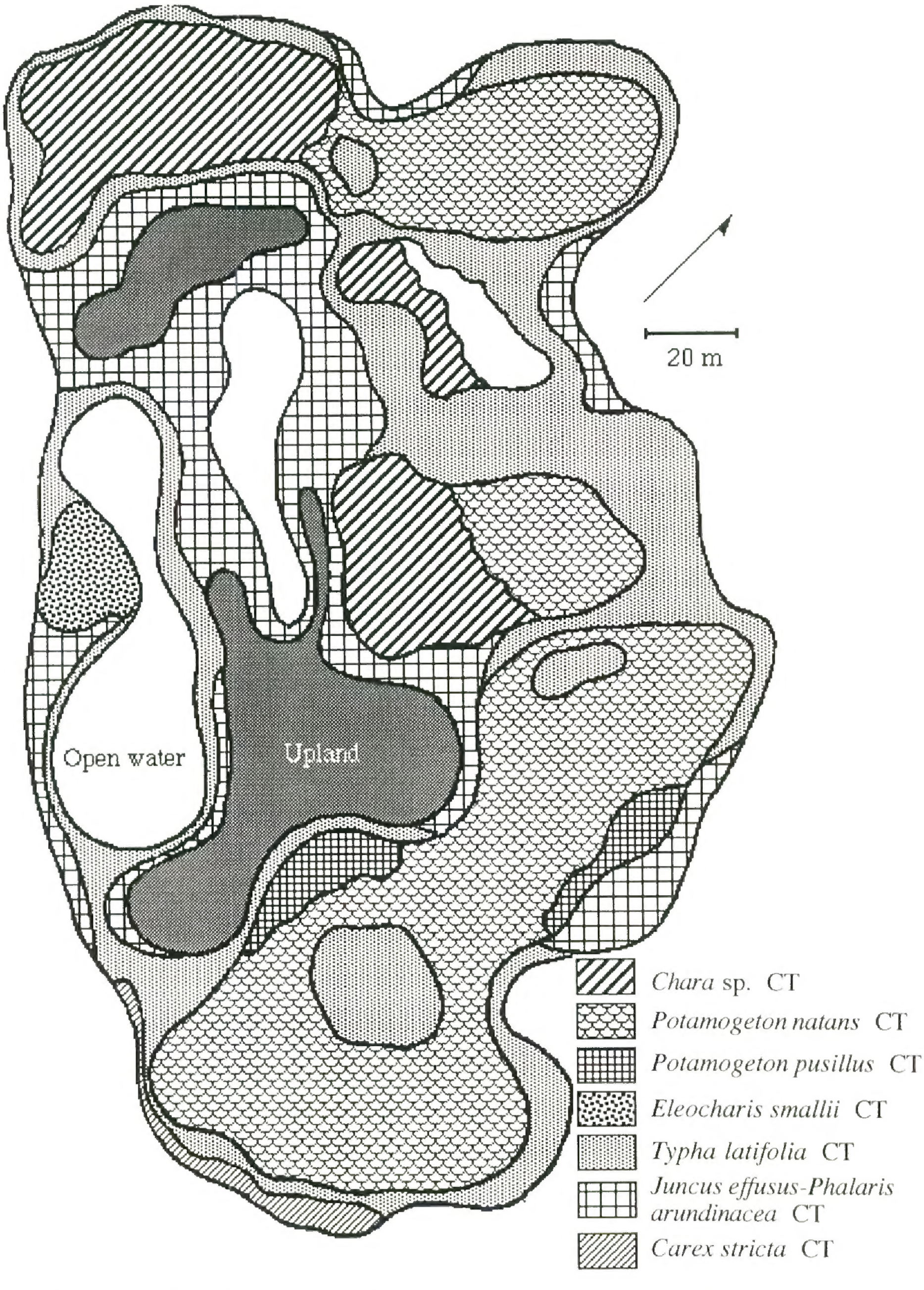

Figure 2. The distribution of the seven plant cover types of the H.C.A. Portsmouth created wetland. CT = Cover type.

Table 1. Mean percent cover and percent frequency for species in the *Potamogeton natans* cover type (species with cover <1 percent are excluded).

Species	% Cover	% Frequency
Potamogeton natans	35	90
Najas minor	11	15
Utricularia gibba	9	82
Potamogeton pusillus	2	15
Eleocharis acicularis	2	6
Lemna minor	1	19
Ludwigia palustris	1	10

of *Chara* were commonly observed as monotypic colonies or with few other species. However, *Utricularia gibba* and *Potamogeton natans* are sub-dominant components of the community. The remaining species of the community (Table 2), with the exception of *P. pusillus,* are more characteristic of emergent areas.

The weedy nature of *Chara* has allowed it to successfully colonize the open water areas of the site. More typically associated with hard water sites, *Chara* has been found to dominate deeper waters of lakes producing large amounts of biomass (Rickett, 1921). The *Chara* community exists in the deeper pools of the wetland, where the cover of floating leaved species is relatively low.

Potamogeton pusillus Cover Type

This cover type is characterized by the submerged Pondweed species, *Potamogeton pusillus* (Table 3). This plant association

Table 2. Mean percent cover and percent frequency for species in the *Chara* cover type (species with cover <1 percent are excluded).

Species	% Cover	% Frequency
Chara cf. *vulgaris*	81	98
Utricularia gibba	11	56
Potamogeton natans	9	37
Eleocharis acicularis	3	7
Ludwigia palustris	1	9
Potamogeton pusillus	1	7
Juncus articulatus	1	4
Typha latifolia	1	4

Table 3. Mean percent cover and percent frequency for species in the *Potamogeton pusillus* cover type (species with cover <1 percent are excluded).

Species	% Cover	% Frequency
Potamogeton pusillus	36	95
Pontederia cordata	12	21
Eleocharis acicularis	5	26
Potamogeton natans	4	47
Utricularia gibba	3	42
Lemna minor	1	37
Najas minor	1	11
Potamogeton amplifolius	1	5

covers the smallest portion of the open water areas and was represented by only 19 quadrats. The *Potamogeton pusillus* cover type occurs in scattered areas within the open water portions of the wetland, most typically close to the emergent vegetation cover types. Two of the largest areas where this cover type is predominate are shown in Figure 2. Although, this cover type is primarily composed of submerged and free-floating species, the emergent *Pontederia cordata* is a sub-dominant component.

EMERGENT COVER TYPES

Juncus effusus-Phalaris arundinacea Cover Type

The *Juncus effusus-Phalaris arundinacea* cover type is the most floristically diverse cover type of the entire wetland. Of the 55 species occurring in the cover type, *Juncus effusus* and *Phalaris arundinacea* are co-dominant, with a collective cover value of 41% (Table 4). This cover type generally extends from the upland shores or islands to the edge communities of the *Typha latifolia* cover type (Figure 2). However, some pool margins are directly surrounded by this cover type where *Typha* does not dominate.

The areas of the *Juncus effusus-Phalaris arundinacea* cover type are rarely inundated for any extended period of time. Most portions remain wet to damp, allowing for a wide range of wetland species to exist. This mostly low-growing, herbaceous plant community has some woody components such as *Alnus incana* ssp. *rugosa, Acer rubrum* and *Cornus* spp. occupying various portions. Unique among cover types, both annuals and perennials are well represented within this association. The Cyperaceae is best repre-

Table 4. Mean percent cover and percent frequency for species in the *Juncus effusus–Phalaris arundinacea* cover type (species with cover <1 percent are excluded).

Species	% Cover	% Frequency
Juncus effusus	21	66
Phalaris arundinacea	20	83
Typha latifolia	6	31
Scirpus cyperinus	6	22
Carex scoparia	4	28
Alnus incana ssp. *rugosa*	4	9
Eleocharis acicularis	3	14
Lemna minor	2	28
Carex lurida	2	14
Acer rubrum	2	8
Cicuta bulbifera	1	28
Galium palustre	1	20
Polygonum amphibium	1	14
Onoclea sensibilis	1	14
Carex vulpinoidea	1	14
Lythrum salicaria	1	11
Polygonum punctatum	1	11
Juncus articulatus	1	9
Typha latifolia	1	9
Ricciocarpus natans	1	8
Eleocharis obtusa	1	6
Spiraea tomentosa	1	6
Eleocharis smallii	1	5
Vaccinium macrocarpon	1	3
Cornus stolonifera	1	3
Cornus amomum	1	2
Potamogeton pusillus	1	2
Solidago rugosa	1	2
Spiraea latifolia	1	2
Thelypteris palustris	1	2

sented in this community. The *Juncus effusus-Phalaris arundinacea* cover type is similar in general physiognomy to the wet-meadow zones or sedge-meadows discussed by Mitsch and Gosselink (1986), by Hammer (1992) and by Weller (1978).

Typha latifolia Cover Type

The Common Cattail cover type represents the second largest community association of the emergent types. Of the 27 species that occur in the cover type, *Typha latifolia* is dominant repre-

Table 5. Mean percent cover and percent frequency for species in the *Typha latifolia* cover type (species with cover <1 percent are excluded).

Species	% Cover	% Frequency
Typha latifolia	25	78
Juncus effusus	6	35
Lemna minor	4	82
Phalaris arundinacea	3	18
Ludwigia palustris	2	29
Utricularia gibba	2	22
Juncus articulatus	2	5
Eleocharis acicularis	1	13
Najas minor	1	14
Acer rubrum	1	2

sented by a 25% cover (Table 5). Sub-dominant components are *Juncus effusus* and *Lemna minor* with covers of six and four percent, respectively.

Typha latifolia and *Lemna minor* have the highest frequencies of occurrence in the cover type. These two species were frequently found associated with each other throughout the wetland, usually with *L. minor* fronds stranded on the wet mud and rhizomes or floating on the still water in between the *T. latifolia* plants. In a survey of southern Wisconsin Cattail marshes, *L. minor* had a frequency of 100%, although its presence was reported as insignificant (Curtis, 1959).

The *Typha latifolia* cover type is the most easily recognizable and discernible of the emergent cover types. This cover type can be quite expansive at certain portions of the wetland, or exist as narrow bands (Figure 2). Several isolated, nearly monotypic, *Typha* "islands" are also present. The dense rhizomatous network produced by *Typha latifolia,* characteristic of the species (McNaughton, 1966), encroaches upon the deeper open water from the very shallow edges. The *Typha latifolia* cover type is similar to the *Typha*-dominated zone typical of freshwater marshes discussed by Mitsch and Gosselink (1986) and by Weller (1978).

The cover type is characterized by species of many growth forms. Important emergent species include *Typha latifolia, Juncus effusus* and *Phalaris arundinacea.* Submergent species include *Utricularia gibba* and *Najas minor,* while the free-floating *Lemna minor,* and the amphibious *Ludwigia palustris* are also components of the cover type.

Table 6. Mean percent cover and percent frequency for species in the *Carex stricta* cover type (species with cover <1 percent are excluded).

Species	% Cover	% Frequency
Carex stricta	58	100
Juncus effusus	6	64
Phalaris arundinacea	6	57
Eleocharis acicularis	6	7
Cicuta bulbifera	4	43
Typha latifolia	3	14
Galium palustre	1	21
Triadenum fraseri	1	7
Spiraea tomentosa	1	7
Typha angustifolia	1	7
Polygonum sagittatum	1	7
Carex lurida	1	7

Carex stricta Cover Type

The Tussock Sedge cover type is one of the smaller emergent plant associations of the wetland. Of the 21 species associated with this cover type *Carex stricta* is dominant, with a 58% cover (Table 6). The raised, wide-spreading tussocks formed by *C. stricta* create a unique, easily discernible cover type. The *Carex stricta* cover type is scattered throughout the wetland, occupying small areas (Figure 2).

Eleocharis smallii Cover Type

The *Eleocharis smallii* cover type occupies the smallest area in the wetland (Figure 2). The cover type was defined by TWINSPAN by the clustering of only nine quadrats and includes 14 species. The dominant species is *E. smallii,* with 27% cover (Table 7). Sub-dominant species are *Typha angustifolia* and *Eleocharis acicularis.* This cover type is scattered throughout the northern portions of the emergent wetland and is also represented by small discontinuous areas intermixed with the *Typha latifolia* and *Juncus effusus-Phalaris arundinacea* cover types.

This cover type is the most floristically unique portion of the wetland. Species typically associated with peatlands, such as *Drosera intermedia, Vaccinium macrocarpon* and *Sphagnum* sp. are part of this community. *Dulichium arundinaceum* and *Viola lanceolata,* also components of the community, were not observed

Table 7. Mean percent cover and mean frequency for species in the *Eleocharis smallii* cover type (species with cover <1 percent are excluded).

Species	% Cover	% Frequency
Eleocharis smallii	27	67
Typha angustifolia	23	56
Eleocharis acicularis	12	22
Vaccinium macrocarpon	9	11
Triadenum fraseri	4	56
Asclepias incarnata	2	11
Lysimachia terrestris	1	33
Lemna minor	1	33
Spiraea tomentosa	1	22
Lythrum salicaria	1	11

growing anywhere else in the wetland. Other species common to this portion of the wetland but observed infrequently elsewhere, are *Asclepias incarnata, Triadenum fraseri, Bidens frondosa* and *Aster racemosus.* The soil of the area is very peaty and is slightly inundated in spring and early summer, but as water table drops later in the summer it becomes merely damp.

RARE PLANT DOCUMENTATION

Two plants listed by Storks and Crow (1978) and the New Hampshire Natural Heritage Inventory (DRED, 1987) as rare for New Hampshire occur at the H.C.A. created wetland, *Sparganium eurycarpum* (threatened) and *Potamogeton foliosus* (endangered). The occurrence of a third, non-indigenous species, *Najas minor,* constitutes the first record of this plant in New Hampshire. Although rare in New Hampshire, both *Sparganium eurycarpum* and *Potamogeton foliosus* are widely distributed throughout the United States (Crow and Hellquist, in press). Both species represent new records for the city of Portsmouth.

Sparganium eurycarpum (Giant Bur-reed) is reported as common along the coastal plain and in western portions of New England (Crow and Hellquist, 1981). There are currently seven documented stations for *Sparganium eurycarpum* in New Hampshire (Natural Heritage Program, pers. comm.). In a study of the rare plants of coastal New Hampshire, *S. eurycarpum* was reported from the towns of New Castle, Rye and Hampton (Dunlop and Crow, 1985). In the study site, *S. eurycarpum* occurs in shallow

water areas along the edges of the pools. The plant was more common along the western edge of the wetland. The water level of this area dropped greatly later in the growing season, leaving the plants growing in damp soils.

In New England *Potamogeton foliosus* (Leafy Pondweed) is reported as being common in calcareous waters of northeastern Maine, Vermont, western Massachusetts and Connecticut (Hellquist and Crow, 1980). Storks and Crow (1978) reported that *P. foliosus* was known from a single station in New Hampshire, in the town of Columbia, Coos County. There are currently five known stations of *P. foliosus* in New Hampshire (Natural Heritage Program, pers. comm.). *Potamogeton foliosus* occurs in the open water areas of the study site. Plants were intermixed with the very similar looking *P. pusillus,* therefore the exact extent of its occurrence is hard to estimate. Other open water macrophytes associated with *P. foliosus* were *P. natans* and *Chara* cf. *vulgaris.* Because Pondweeds are heavily consumed by waterfowl (Martin, 1951; Fassett, 1957), *P. foliosus* was most likely introduced into the study site by ducks or other waterfowl.

A third new record for the flora of Portsmouth, the adventive *Najas minor,* is also the first record for New Hampshire (Padgett and Crow, 1993). A European native, *Najas minor* (Eutrophic Water-nymph) was first reported in America in the Hudson River, in 1934 (Clausen, 1936). The North American range of this introduced species has continued to spread steadily in the eastern United States. By 1968, *N. minor* was known from New York, Pennsylvania, Illinois, West Virginia, Tennessee, Alabama and Florida (Merilainen, 1968). Its present North American distribution extends from New England and New York west to Illinois, south to Florida, Mississippi and Arkansas (Haynes, 1979; Crow and Hellquist, in press). The first report for this plant in New England was in 1965, occurring in Lake Champlain at New Haven, Vermont. Two reports of the species occurring in Bershire County, Massachusetts followed in 1974 (Hellquist, 1977). Hellquist and Crow (1980) report the distribution of *N. minor* to be infrequent in waters of extreme western New England. The present discovery of *N. minor* in New Hampshire possibly represents the northeastern-most range extension to date of the species for the U.S.

At the H.C.A. created wetland, *Najas minor* occurs in the open water areas. A component of the strictly aquatic macrophyte com-

munity of the site, *N. minor* is commonly associated with *Potamogeton pusillus, P. natans, Utricularia gibba* and *Chara* cf. *vulgaris* Later in the summer, many plants became fragmented and consequently were floating at the water surface and near the pool margins.

Najas minor is an annual, producing large quantities of seed. The most important dispersal agent for *N. minor* is waterfowl who feed heavily on the entire plant. Interestingly, the pattern of distribution of *N. minor* is very similar to the Atlantic flyway pattern of migrating waterfowl (Merilainen, 1968). Therefore it is believed that *N. minor* was probably introduced into the site by waterfowl. *Najas minor* has also been reported to invade recently constructed artificial lakes and ponds (Wentz and Stuckey, 1971).

FLORA OF H.C.A. PORTSMOUTH CREATED WETLAND

The vascular flora of the H.C.A. Portsmouth created wetland consists of 104 species, belonging to 69 genera and 45 families. Fifty-six species are dicots and forty-four species are monocots. The dominant families are the Asteraceae, Cyperaceae and Poaceae.

POLYPODIOPHYTA

DRYOPTERIDACEAE

Onoclea sensibilis L. Sensitive Fern

Abundant; throughout the wetland on wet soil. *Padgett 59, 145.*

OSMUNDACEAE

Osmunda regalis L. Royal Fern

Uncommon; on western edge of wetland growing on embankment. *Padgett 138.*

THELYPTERIDACEAE

Thelypteris palustris Schott Marsh Fern

Occasional; along the shores of the wetland but locally abundant along the western shore. *Padgett 92, 160, 231.*

EQUISETOPHYTA

EQUISETACEAE

Equisetum arvense L. Common Horsetail
Common; throughout the wetland on wet or moist soils. *Padgett 56, 81.*

MAGNOLIOPHYTA

DICOTYLEDONS

ACERACEAE

Acer rubrum L. Red Maple
Common; throughout the emergent wetland as seedlings, but more occasional as young trees. *Padgett 87.*

APIACEAE

Cicuta bulbifera L. Bulbiferous Water-hemlock
Common; throughout the wetland growing in emergent areas. *Padgett 68, 158, 183, 217.*

Sium suave Walter Water-parsnip
Uncommon; growing in wet emergent areas. *Padgett 216.*

AQUIFOLIACEAE

Ilex verticillata (L.) A. Gray Winterberry
Occasional; growing in wooded areas within the wetland. *Padgett 235.*

ASCLEPIADACEAE

Asclepias incarnata L. subsp. *pulcra* (Ehrh. ex. Willd.) Woodson Swamp Milkweed
Occasional; throughout the emergent wetland, but locally abundant in the western shore area. *Padgett 86, 121.*

ASTERACEAE

Aster lanceolatus var. *simplex* (Willd.) A. G. Jones Eastern Lined Aster
Uncommon; along western side of wetland. *Padgett 237.*

Aster racemosus Ell. Small White Aster
Uncommon; growing around the western shore area. *Padgett 252.*

Bidens connata Muhl. Purplestem Beggar-ticks
Ocassional; in emergent areas, but more common in the western area. *Padgett 218, 234, 245, 246, 253, 256, 261.*
Bidens frondosa L. Devil's Beggar-ticks
Uncommon; in emergent area of the western shore. *Padgett 233.*
Eupatorium perfoliatum L. Boneset
Occasional; growing along wet shores and emergent areas of the wetland. *Padgett 198.*
Euthamia graminifolia (L.) Nutt. Common Flat-topped Goldenrod
Occasional; growing along the shores of the wetland. *Padgett 222.*
Solidago rugosa Miller subsp. *rugosa* Wrinkle-leaved Goldenrod
Occasional; growing along the shores and scattered in the emergent areas. *Padgett 181.*

BALSAMINACEAE
Impatiens capensis Meerb. Orange Touch-me-not
Occasional; throughout the northern emergent areas and outermost shores. *Padgett 175.*

BETULACEAE
Alnus incana (L.) Moench. subsp. *rugosa* (Du Roi) Clausen Speckled Alder
Frequent; growing along outer shores and wooded areas. *Padgett 76, 101.*

CALLITRICHACEAE
Callitriche verna L. Water Starwort
Uncommon; growing in shallow water areas along the shores. *Padgett 58, 187.*

CLUSIACEAE
Hypericum boreale (Britt.) Bickn. St. John's-wort
Uncommon; growing in emergent marsh areas. *Padgett 228.*
Hypericum canadense L. Narrow-leaved St. John's-wort

Uncommon; growing in emergent marsh areas. *Padgett 204.*

Hypericum dissimulatum Bickn. St. John's-wort

Locally abundant; in western open marsh area and along northwestern shore. *Padgett 227.*

Hypericum ellipticum Hook. St. John's-wort

Common; throughout the emergent areas and in shallow water. *Padgett 139, 156.*

Hypericum mutilum L. Dwarf St. John's-wort

Occasional; throughout the emergent marsh. *Padgett 201.*

Triadenum fraseri (Spach) Gleason Marsh St. John's-wort

Common; throughout the emergent areas but more frequent in the open area of the western side. *Padgett 94, 146, 195, 260.*

CORNACEAE

Cornus amomum subsp. *obliqua* (Raf.) J. S. Wilson Silky Dogwood

Uncommon; growing along outer southwestern shore. *Padgett 104.*

Cornus stolonifera Michx. Red-stemmed Dogwood

Occasional; growing in emergent and wooded areas, but more common in the western open marsh area. *Padgett 89, 151.*

DROSERACEAE

Drosera intermedia Hayne Sundew

Locally abundant; growing in wet open area of western side of the wetland. *Padgett 95, 147.*

ERICACEAE

Lyonia ligustrina (L.) DC. Maleberry

Occasional; in wooded areas throughout the wetland. *Padgett 230.*

Vaccinium corymbosum L. Highbush Blueberry

Uncommon; in wooded areas on western side of wetland. *Padgett 155.*

Vaccinium macrocarpon Aiton Cranberry

Locally abundant; in open area of western shore and grow-

ing with *Typha latifolia* in northern area of wetland. *Padgett 90, 140.*

HALORAGACEAE

Proserpinaca palustris L. Common Mermaid-weed

Uncommon; in open water areas close to the shores. *Padgett 69, 125.*

LAMIACEAE

Lycopus americanus Muhl. Bugle-weed

Occasional; throughout the emergent marsh. *Padgett 205.*

Lycopus uniflorus Michx. Bugle-weed

Common; throughout the emergent marsh. *Padgett 240.*

Scutellaria galericulata L. Common Scullcap

Uncommon; growing in wet mud of northwestern shore. *Padgett 208.*

LENTIBULARIACEAE

Utricularia gibba L. Creeping Bladderwort

Abundant; in open water areas throughout the wetland. *Padgett 57, 133.*

Utricularia minor L. Lesser Bladderwort

Uncommon; growing in very shallow pools floating on surface between other vegetation. *Padgett 250.*

LYTHRACEAE

Lythrum salicaria L. Purple Loosestrife

Common; throughout the emergent marsh areas. *Padgett 75, 114, 124.*

MYRICACEAE

Myrica gale L. Sweet Gale

Uncommon; in emergent wetland at island shore edge of northern area. *Padgett 191.*

NYMPHAEACEAE

Nuphar variegata Durand Yellow Water-lily

Occasional; in open water areas close to shores. *Padgett 126.*

ONAGRACEAE

Epilobium palustre L. Marsh Willow-herb

Uncommon; growing in emergent marsh areas. *Padgett 221.*

Ludwigia palustre (L.) Elliott. Common Water-purslane

Frequent; growing throughout the open water areas and on the muddy bottoms of the emergent areas. *Padgett 63, 129.*

POLYGONACEAE

Polygonum amphibium L. var. *emersum* Michx. Water Smartweed

Common; throughout the marsh on the elevated islands and emergent areas. *Padgett 148, 180, 238, 247.*

Polygonum arifolium L. Tearthumb

Occasional; growing with *Polygonum sagittatum. Padgett 193.*

Polygonum lapathifolium L. Pale Smartweed

Uncommon; growing on a beaver den in northern area. *Padgett 172.*

Polygonum punctatum Ell. var. *punctatum* Water Smartweed

Frequent; throughout the open emergent wetland. *Padgett 186, 190.*

Polygonum sagittatum L. Arrow-vine

Common; at the edges of the open water areas. *Padgett 179, 185.*

Rumex crispus L. Curly Dock

Uncommon; at the northern edge of the wetland. *Padgett 177.*

PRIMULACEAE

Lysimachia terrestris (L.) BSP. Bulbil-loosestrife

Frequent; throughout the emergent wetland. *Padgett 152, 219, 239, 242.*

ROSACEAE

Spiraea latifolia (Aiton) Borkh. Meadowsweet

Uncommon; throughout emergent areas of the wetland. *Padgett 85.*

Spiraea tomentosa L. Hardhack

Common; throughout emergent areas, but more frequent in open western area. *Padgett 91, 137.*

RUBIACEAE

Galium palustre L. Marsh Bedstraw

Common; growing in the lower parts of the emergent vegetation throughout the wetland. *Padgett 83.*

SALICACEAE

Salix nigra Marshall Black Willow

Uncommon; growing along the northern and western outer shores. *Padgett 200.*

SAXIFRAGACEAE

Penthorum sedoides L. Ditch-stonecrop

Occasional; growing in open emergent areas and cattail stands of western side of wetland. *Padgett 207.*

SCROPHULARIACEAE

Agalinis purpurea (L.) Pennell Purple Gerardia

Uncommon; growing in marsh area along the western limits of the wetland. *Padgett 214.*

Mimulus ringens L. Monkey Flower

Occasional; growing in emergent marsh areas throughout the northern half of the wetland. *Padgett 165, 178.*

SOLANACEAE

Solanum dulcamara L. Bittersweet

Occasional; throughout the emergent wetland. *Padgett 62, 113.*

URTICACEAE

Boehmeria cylindrica (L.) Sw. Bog Hemp

Uncommon; growing along outer edge of wetland in northwest area. *Padgett 257.*

VERBENACEAE

Verbena hastata L. Blue Vervain

Uncommon; growing along the outer edges of the wetland. *Padgett 203.*

VIOLACEAE

Viola lanceolata L. Strap-leaved Violet

Locally abundant; growing in moist soil of western open marsh area. *Padgett 255.*

Monocotyledons

ALISMATACEAE

Alisma triviale Pursh. Northern Water-plantain

Occasional; growing in muddy substrate throughout the wetland. *Padgett 96, 166.*

Sagittaria latifolia Willd. Common Arrow-head

Occasional; in shallow water at southwest end of wetland. *Padgett 97, 176.*

CYPERACEAE

Carex comosa Boott Long-hair Sedge

Common; throughout the emergent areas of the wetland. *Padgett 67, 107, 144.*

Carex lurida Wahl. Lurid Sedge

Common; Throughout the emergent areas of the wetland. *Padgett 98, 168.*

Carex lupulina Willd. Hop Sedge

Uncommon; in emergent area along western perimeter. *Padgett 258.*

Carex pseudocyperus L. Cyperus-like Sedge

Common; throughout the emergent areas of the wetland. *Padgett 132.*

Carex scoparia Schk. Broom Sedge

Frequent; throughout the emergent areas of the wetland. *Padgett 70, 109.*

Carex stricta Lam. Tussock Sedge

Occasional; along the outer shore edges and emergent marsh areas. *Padgett 72.*

Carex vulpinoidea Michx. Fox Sedge

Frequent; throughout the emergent areas of the wetland. *Padgett 143, 154.*

Cyperus strigosus L. Umbrella Sedge

Uncommon; growing along western and northern shores. *Padgett 196.*

Dulichium arundinaceum (L.) Britt. Three-way Sedge

Locally abundant; growing in open marsh area of western shore. *Padgett 215.*

Eleocharis acicularis (L.) R.&S. Needle-rush

Common; growing along muddy shores and throughout the emergent marsh. *Padgett 99, 173.*

Eleocharis obtusa (Willd.) Shultes Blunt Spike-rush

Common; growing throughout emergent marsh areas and shallow pools. *Padgett 169.*

Eleocharis smallii Britt. Small's Spike-rush

Occasional; throughout the emergent areas, but more locally abundant growing out of shallow pools of western half of wetland. *Padgett 73.*

Eleocharis tenuis (Willd.) Shultes var. *tenuis* Slender Spike-rush

Occasional; in wet mud open areas or below *Typha latifolia* stands. *Padgett 170.*

Rhynchospora capitellata (Michx.) Vahl. Beakrush

Uncommon; growing in wooded area of northwestern region of wetland. *Padgett 226.*

Scirpus atrocinctus Fern. Black-girdle Bulrush

Uncommon; growing along northern and southern outer limits of wetland. *Padgett 159.*

Scirpus cyperinus (L.) Kunth. Wool Grass

Frequent; Growing in emergent areas throughout the wetland. *Padgett 161, 189.*

Scirpus hattorianus Makino

Uncommon; growing along outer limits of the wetland. *Padgett 150, 225.*

Scirpus pungens Vahl. Three-square Bulrush

Uncommon; growing in wet soil along the northwestern shore. *Padgett 194.*

Scirpus tabernaemontanii K.C. Gmel. (= *S. validus* Vahl) Great Soft-stem Bulrush

Frequent; throughout the emergent wetland. *Padgett 112, 122.*

IRIDACEAE

Iris versicolor L. Northern Blue Flag

Uncommon; growing along the edges of open pools around the islands. *Padgett 115, 136.*

JUNCACEAE

Juncus articulatus L. Jointed Rush

Frequent; throughout the emergent wetland. *Padgett 131, 135, 163, 171, 188.*

Juncus canadensis J. Gay Canada Rush

Occasional; throughout the emergent wetland. *Padgett 223, 224.*

Juncus effusus L. Soft Rush

Abundant; throughout the emergent wetland. *Padgett 66, 80, 111, 117.*

LEMNACEAE

Lemna minor L. Common Duckweed

Abundant; floating on surface throughout the open water and *Typha* stands. *Padgett 116.*

Wolffia columbiana Karst. Water-meal

Uncommon; floating on surface in open water with *Lemna minor* at north end of study site. Site Record.

NAJADACEAE

Najas minor Allioni. Eutrophic Water-nymph

Common; in open water with *Chara* cf. *vulgaris Padgett 167, 236.*

POACEAE

Calamagrostis canadensis (Michx.) Beauv. Reed Bent Grass

Common; in emergent areas around the perimeter of the wetland. *Padgett 120, 153, 251.*

Echinochloa crusgalli (L) Beauv. Barnyard Grass

Uncommon; in emergent marsh areas. *Padgett 213, 248.*

Glyceria canadensis (Michx.) Trin. Rattlesnake Manna Grass

Uncommon; along outer edge of the western shore. *Padgett 259.*

Leersia oryzoides (L.) Sw var. *oryzoides* Rice Cut Grass
Common; in emergent marsh areas. *Padgett 241, 249.*
Panicum villosissimum Nash. Panic Grass
Uncommon; growing in open areas adjacent with upland islands. *Padgett 192.*
Panicum rigidulum Nees. Panic Grass
Uncommon; in emergent marsh areas. *Padgett 244.*
Phalaris arundinacea L. Reed Canary Grass
Frequent; growing along the outer edges of the wetland. *Padgett 60, 65, 93, 108, 119, 162.*
Poa palustris L. Fowl Bluegrass
Occasional; in open marsh areas. *Padgett 174.*

PONTEDERIACEAE

Pontederia cordata L. Pickerel-weed
Occasional; in shallow open water areas close to the shore, forming dense stands. *Padgett 102, 123.*

POTAMOGETONACEAE

Potamogeton amplifolius Tuckerman Big-leaf Pondweed
Uncommon; in open water area with *Potamogeton natans* at southeast end of wetland. *Padgett 127.*
Potamogeton foliosus Raf. var. *foliosus* Leafy Pondweed
Frequent; in open water areas throughout the wetland. *Padgett 164.*
Potamogeton natans L. Floating Pondweed
Abundant; throughout open water areas. *Padgett 57, 74, 130.*
Potamogeton pusillus L. var. *tenuissimus* Mert. and Koch Slender Pondweed
Frequent; in open water areas throughout the wetland. *Padgett 118, 128.*

SPARGANIACEAE

Sparganium eurycarpum Engelm. Giant Bur-reed
Common; in shallow water areas throughout the marsh, but more frequent along the western edge of the wetland. *Padgett 53, 88.*

TYPHACEAE

Typha angustifolia L. Narrow leaved Cattail

Occasional; growing intermixed with *Typha latifolia* along pool edges and in thick stands. *Padgett 77, 142.*

Typha latifolia L. Common Cattail

Abundant; throughout the wetland, often encroaching the open pools. *Padgett 78.*

In conclusion, the vegetation component of this relatively young created wetland appears to be quite heterogeneous with a diverse floristic composition comprising seven discernible vegetation cover types. One hundred and four vascular plant species are documented from the wetland including two species listed as rare for New Hampshire and the first state record for an introduced weedy species. What makes this site remarkable is that although it is floristically diverse there was no direct planting of wetland plants during its construction. The challenge of establishing diverse, functional wetland plant communities at this site appears to have been met essentially by the transplantation of wetland muck. This point should be stressed for future considerations in mitigation project planning.

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DEPARTMENT OF PLANT BIOLOGY
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NEW HAMPSHIRE 03824

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OBSERVATIONS ON REPRODUCTION IN *TRIPHORA TRIANTHOPHORA* (ORCHIDACEAE)

SUSAN A. WILLIAMS

ABSTRACT

A small population of the orchid *Triphora trianthophora* in western Massachusetts was investigated over a six-year period (1988 through 1993). Observations on the flowering habits and seed capsule production are described, as well as vegetative reproduction by means of tuberoids. *Triphora* produces an abundance of short-lived flowers yet very few capsules are initiated. The majority of *Triphora*'s existence is spent underground reproducing asexually by means of new tuberoids.

Key Words: *Triphora trianthophora*, orchid, tuberoids

INTRODUCTION

Triphora trianthophora is a small woodland orchid, elusive and secretive, appearing abundantly one year and rare or absent for many succeeding years (Lownes, 1920; Ames, 1948; Sheviak, 1974; Brackley, 1981). *Triphora trianthophora* also shows synchronous flowering, the majority of its short-lived flowers appear 48 hours after a temperature drop (Brackley, 1981; Keenan, 1986, 1988; Sheviak, 1974). In fact, all species of *Triphora* which are not self-pollinating exhibit gregarious flowering (Dressler, 1981) apparently to increase their chances of cross-pollination (Luer, 1975). Even so, *Triphora trianthophora* rarely sets seed (Lownes, 1920; Keenan, 1992).

The most unusual feature of this orchid, however, is its existence for years at a time in a subterranean, tuberous condition (Lownes, 1920; Ames, 1948; Zavitz and Gaiser, 1956). Although the tribe Triphoreae appears to be a relic group with no close allies, it does share a unique feature with members of the tribes Orchideae, Diseae and Diurideae in having these root-stem tuberoids (Dressler, 1981). I started observing the underground tuberoids of *Triphora* in part because of a statement made by Oakes Ames in 1948 in that he supposed there was a ". . . maximum size for the tubers that bear flowering stems." Every plant of *T. trianthophora* has from one to numerous tuberoids attached by stolons. These tuberoids are thickened underground storage structures superficially similar to tubers, but structurally different. As Dressler (1981) points out, true tubers are not found in orchids.

The primary tuberoid contains the apical bud which may form a new shoot in the growing season. Axillary buds form secondary tuberoids at the end of slender stolons. These secondary tuberoids continue to increase in size with the age of the plant, along with increasing length of the stolon. The stolon tends to grow downwards into the leaf litter so that with accumulating litter accounts for the depth of the primary tuberoids. These secondary tuberoids on becoming detached from the parent plant form primary tuberoids of new plants with the same genotype as the parent.

Most plants, however, do not form flowering shoots but remain in the leaf litter (pers. obs.), and these plants consist of primary and secondary tuberoids as seen in Figure 4a and 4b.

This paper presents the observations gathered over six years on: 1) sexual reproduction in *Triphora trianthophora,* in particular the reason for low capsule set; and 2) vegetative reproduction in *Triphora,* particularly the underground growth form with possible correlations to population fluctuations, and the relationship between primary tuberoid size and the plant's reproductive status.

METHODS

I became acquainted with *Triphora trianthophora* in 1988, when I began studies on a small population in western Massachusetts for the Massachusetts Natural Heritage and Endangered Species Program.

The study site comprises an area of approximately two acres of northern hardwood forest dominated by *Fagus grandifolia* and *Acer saccharum.* The site is on a southeast facing slope at an elevation of 900–1100 feet. It is midslope being approximately 300 feet above the Deerfield River basin.

The study area was subdivided into distinct sites where the plants were located. In 1988 there were 25 sites and in each succeeding year I found additional sites until there were a total of 72 sites in 1993, all within the general area. The cumulative total of vegetative and reproductive plants observed over the six year period was 1448.

I observed the plants on a daily basis for their entire aboveground existence of approximately one month, from their first emergence through the litter, to capsule set. Each site was monitored for the total number of plants; number of vegetative plants;

plants which produced buds but failed to blossom (in all cases this was due to some type of herbivory); plants which blossomed but did not initiate a seedpod; and plants which ripened seedpods. Percent capsule set was determined by the ratio of capsules set to total buds produced by the population.

While collecting data on each site, any pollinators or floral visitors were noted, and also whether the plants had undergone any type of herbivory.

A few plants that did not produce capsules were carefully removed from the litter and the length of their primary tuberoid was measured. This group included small primary tuberoids which had never produced any stem; tuberoids with hyaline stems (fragile, translucent stems remaining under the litter not producing leaves or flowers but with one or more secondary tuberoids attached); vegetative plants (those having above-ground stems with one small leaflet but no flowers); and plants with one, two, three, or four flowers.

As I started removing litter I also noted many other tuberoids in the same vicinity that had produced neither leafy nor flowering stems. These consisted of a primary tuberoid and one to many secondary tuberoids. Some had hyaline stems with secondary tuberoids but had never produced above-ground stems. Many large tuberoids were also noted which had previously produced above-ground stems but had not produced any in the current year. These tuberoids were not measured. Due to the invasive nature of measuring primary tuberoid length, only a small sample was measured each year.

A yearly comparison was made of the total number of plants for the original 25 sites as well as comparing fluctuations within individual sites.

RESULTS

Observations on Sexual Reproduction

Throughout the six-year study period, the majority of *Triphora trianthophora* plant produced flower-bearing stems; only 10% or less failed to flower in any given year. (Figure 1). Most of the plants bore one or two flowers; those having three of four were much less frequent totaling less than 10% in any given year. This pattern remained relatively constant over six years.

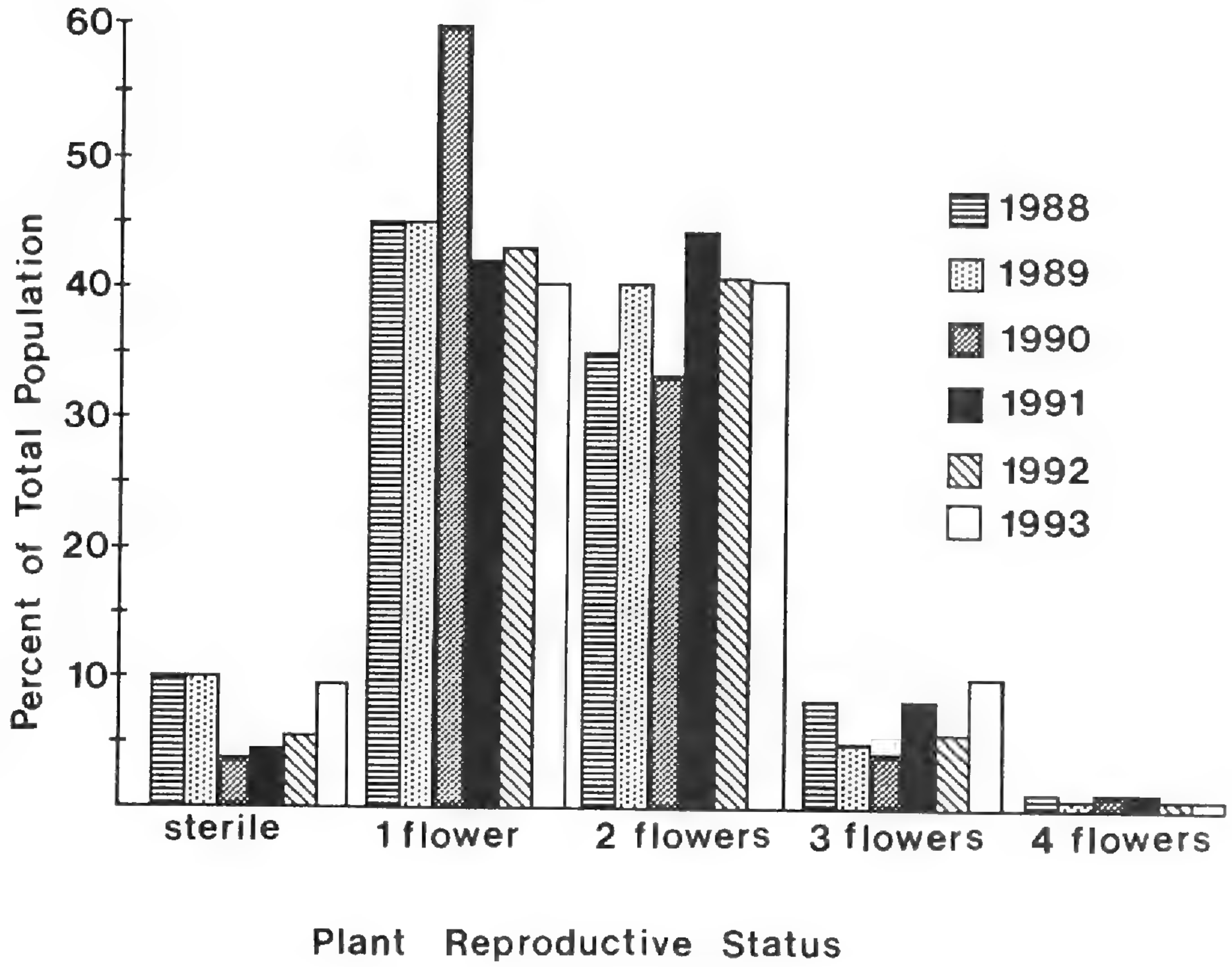

Figure 1. Percentages of plants of differing reproductive status in a *Triphora* population over a six-year period.

Figure 2 illustrates on a yearly basis the percentages of bud loss, flowers produced and capsules ripened out of the total bud population.

The large percentage of buds lost was caused by several factors. Rarely, a few buds would be underdeveloped and tiny and these would always drop off prior to flowering. Occasionally, entire plants had been consumed by chipmunks (their tunnels were found under clumps of *Triphora* plants) and no trace of plant or tuberoids could be found. Slugs were the most destructive herbivores of *Triphora*. Stems were chewed through, usually at litter level, and the plants would be lying on the ground. Sometimes, they were chewed in half higher up and occasionally the buds were half eaten. I noted slugs in the upper litter layers many times and observed slugs on *Triphora* plants (including the tuberoids) several times.

Also illustrated in Figure 2 is that capsule production relative to total buds produced is very low. However, out of 110 capsules

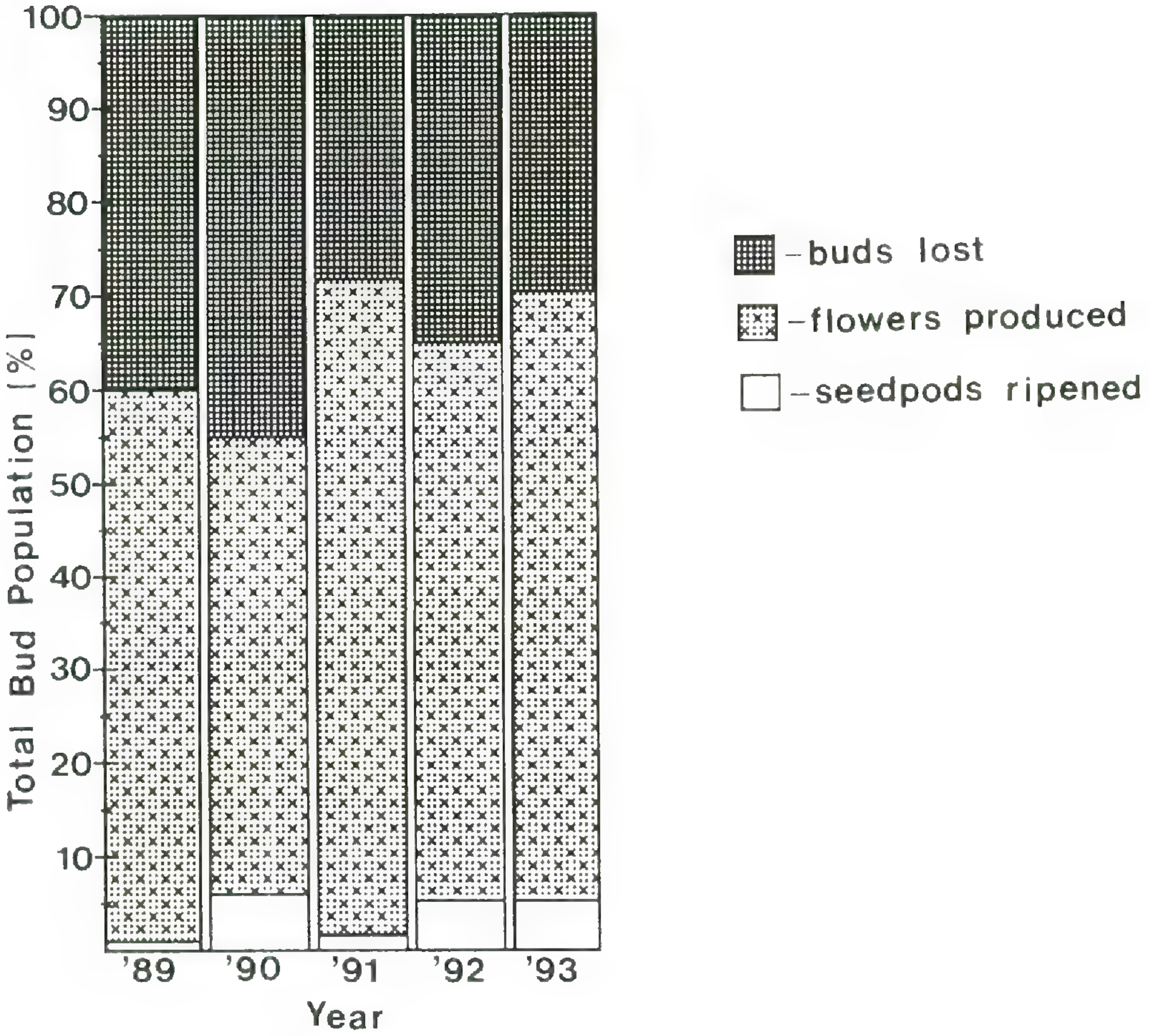

Figure 2. Percentages of buds lost, flowers produced and seedpods ripened out of the total bud population, compared yearly.

initiated 104 ripened, which is 95%. The other 6 did not ripen because of loss of the plant due to herbivory.

It appears that few of the flowers are actually pollinated, supported by the fact that on only two occasions in six years did I note any floral visitors. One appeared to be a small species of bumblebee (*Bombus*) which entered the blossom for a few seconds, then backed out with pollinia attached. The only other flower visitor I observed was a much smaller and slender bee probably belonging to the genus *Hylaeus*. I did not observe any pollinia removal with its visit, but whether the bee was too small or the pollinia had already been removed could not be determined.

Another factor contributing to low capsule set is the fact that the *Triphora* blossom is available to pollinators for one day only. The day following a bloom shows noticeable fading and drooping

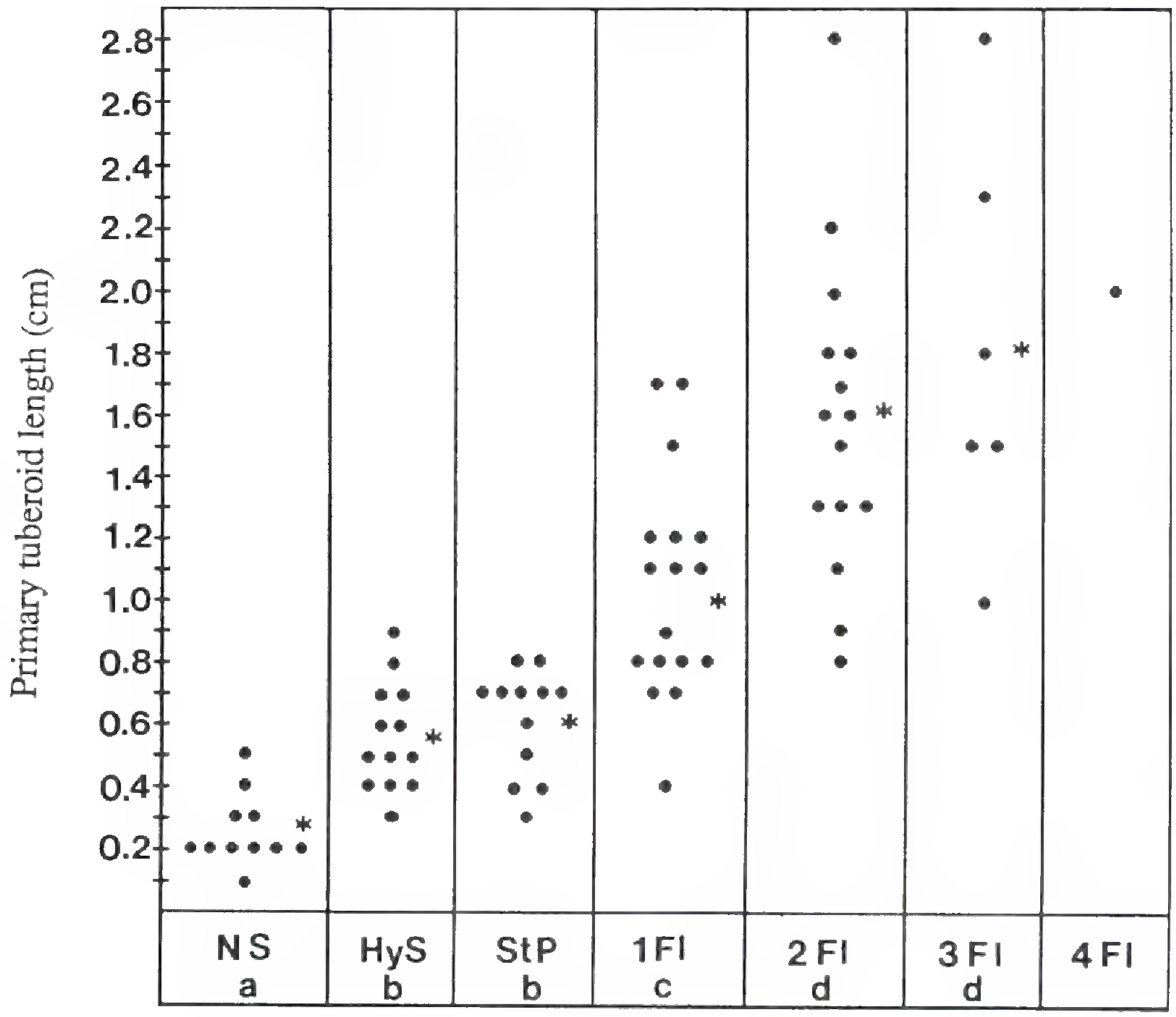

Figure 3. Relationship of primary tuberoid length (cm) to reproductive status of plant. NS—No Stem; HyS—Hyaline Stem; StP—Sterile Plant; 1 Fl—one flower; 2 Fl—two flowers; 3 Fl—three flowers; 4 Fl—four flowers. Each dot represents an individual plant. Asterisks represent the mean of the group. Different letters indicate a significant difference between the means. (Bonferroni adjustment, P = .05)

until, after an average of five days, the blossom falls off the plant. If the flower is fertilized, the ovary starts to swell and the dried corolla remains intact.

Observations on Vegetative Reproduction

Although the stimulus for shoot production in *Triphora* is as yet unclear, Figure 3 shows the relationship between primary tuberoid size and type of plant. Plants that consisted of a primary

Table 1. One-way analysis of variance of reproductive status. The length data were log transformed to homogenize the variance and the log of length was then used as the dependant variable.

	Analysis of Variance				
Source	Sum-of-Squares	df	Mean-Square	*F*-Ratio	*P*
Reproductive status	29.766019	5	5.953204	47.560594	0.000000
Error	8.511623	68	0.125171		

tuberoid with no shoot development had the smallest primary tuberoids; those plants with either hyaline stems or sterile leaflets had slightly larger primary tuberoids; and primary tuberoid size tended to increase with increasing numbers of flowers per plant. A one-way ANOVA was done on the data with the log of length as the dependent variable. The length data were log transformed in order to homogenize the variances. As seen from the ANOVA table (Table 1), the developmental classes showed significant variation in tuberoid length. In order to analyze the variation between classes, a Bonferroni Adjustment was done. The results (shown by the letters in Figure 3) indicated which classes varied significantly from which other class.

The primary tuberoid is generally the largest and the deepest down in the litter from which the flowering stem and secondary tuberoids arise (*see* Figure 4). The secondary tuberoid closest to the primary tuberoid is the largest with smaller tuberoids appearing up the stem. There are many variations in the number of secondary tuberoids and their arrangement on any individual plant. Some plants have only one secondary tuberoid, in others I have counted up to 17. However, all plants have at least one. Occasionally the secondary tuberoids get quite large before becoming separated from the main plant. Several secondary tuberoids were even slightly larger than the primary tuberoid. There doesn't appear to be a specific size when the stolon disintegrates between the main plant and the secondary tuberoids. More likely, they separate as a result of physical forces since they are fragile and near the litter surface. The tuberoids remain in the leaf litter never reaching into the soil substrate.

Another distinct difference between primary and secondary tuberoids is that the primary tuberoid is a tan color whereas all secondary tuberoids are waxy white. I found tiny primary tuber-

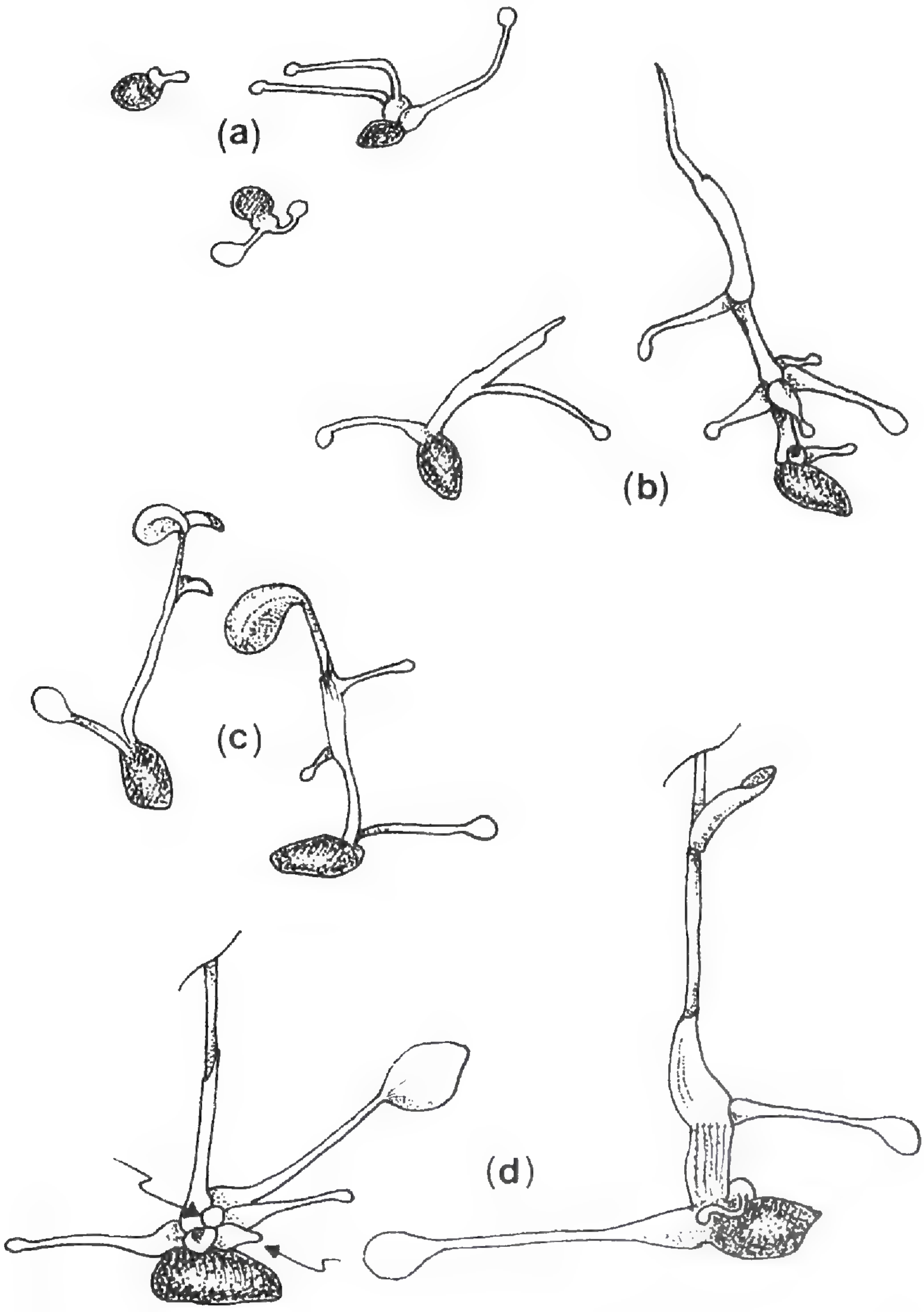

Figure 4. Variation in primary and secondary tuberoid growth in successive stages of *Triphora* development. (a) small primary tuberoids with secondary tuberoid development but no stem development; (b) hyaline stem production; (c) leaflet of a non-flowering shoot; (d) flowering plants (arrows show swellings near primary tuberoid which will develop into secondary tuberoids).

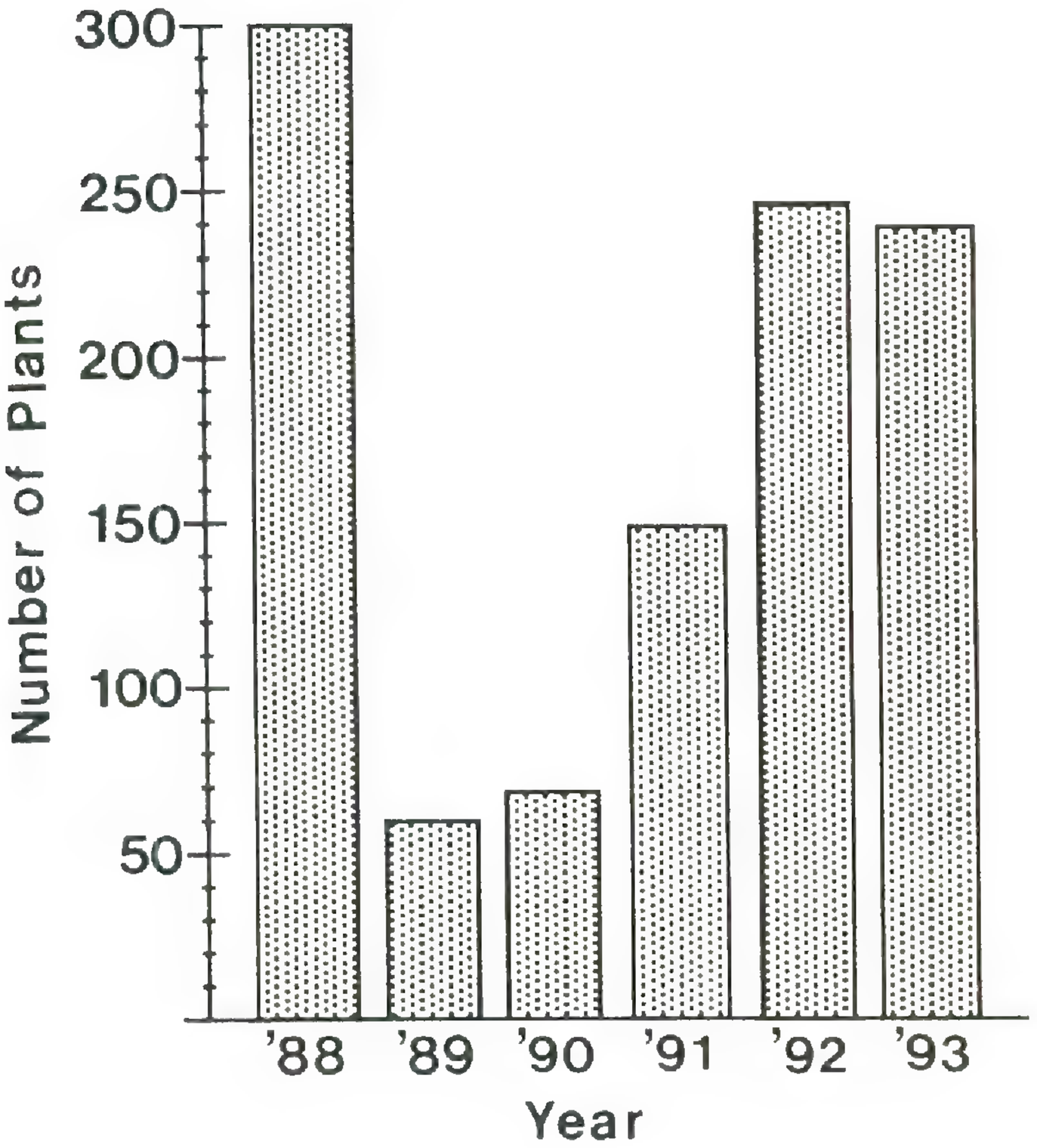

Figure 5. Fluctuations in the total population from 1988 through 1993 on the original 25 sites.

oids in the litter only 1 mm long, some of which were already producing a new secondary tuberoid.

Figure 5 shows the yearly fluctuations in population size for the original 25 sites found in 1988. It suggests a pattern of increasing and decreasing population size, but more data is needed to confirm this.

Table 2 shows the fluctuations of plants within each of the 25 sites over the six years. There is not only a great deal of variation in plant numbers between sites but also within individual sites on a year-to-year basis. What the Table doesn't show is that plants that reappear are not always in the same location as in previous years even though they are in the same site. This indicates that there are many primary tuberoids existing in the litter without producing shoots for years at a time.

Due to this sporadic shoot production, it is very difficult to assess population size and vigor. Their absence for many years does not mean they are not there. I confirmed this by removing

Table 2. Actual numbers of vegetative and flowering plants for each of the original 25 sites and their yearly fluctuations.

	Total Number of Plants					
Site #	1988	1989	1990	1991	1992	1993
1	4	0	0	0	0	0
2	8	0	6	4	9	11
3	4	0	0	0	0	1
4	3	0	0	0	0	0
5	7	0	2	2	0	0
6	8	2	1	5	0	1
7	1	0	0	1	0	13
8	There is no site #8					
9	14	2	0	8	5	2
10	10	0	0	6	2	0
11	28	1	4	2	11	10
12	1	0	0	0	0	0
13	2	1	0	0	0	0
14	3	0	0	0	2	0
15	11	2	0	0	0	0
16	19	5	7	9	20	18
17	13	0	1	2	8	14
18	20	3	0	22	35	36
19	22	7	1	4	2	3
20	23	4	6	18	19	8
21	37	21	30	61	113	93
22	47	0	4	1	3	19
23	7	0	2	2	3	6
24	5	1	0	1	0	0
25	3	2	1	0	11	5
Total	300	51	65	148	243	240

litter in several potential sites in 1989 where I had never observed *Triphora*. In three of the sites I found numerous tubers and in 1990 these areas contained 21 flowering plants.

DISCUSSION

Triphora trianthophora is a species of the climax hardwood forest always associated with *Fagus grandifolia* (Lownes, 1920; Zavitz and Gaiser, 1956; Sheviak, 1974; Crow and Stokes, 1980; Brackley, 1981; Martin, 1983; Keenan, 1992). It initiates shoot growth and flowers in August when the herbaceous environment under a full canopy is characterized by very low light levels,

highest soil temperatures, and lowest nutrient and water availability due mainly to uptake by trees (Mahall and Bormann, 1978). Many of the ground herbs here are spring ephemerals which complete their life cycles prior to canopy closure. Early leaf and flower production may be the result of selection for completing these processes while light intensity at the forest floor is high and could be viewed as a method by which plants reduce interspecific competition (Newell and Tramer, 1978).

It has also been shown that spring ephemerals lack the capacity to modulate their photosynthetic and respiratory physiology in response to decreased light levels accompanying canopy closure. This lack of adaptability limits the ephemerals from exploiting reduced light environments and consequently ephemerals revert to a dormant condition soon after the canopy species leaf out (Chabot and Mooney, 1985).

Shade tolerant species such as *Triphora* carry out most of their growth and photosynthesis under a closed canopy. *Triphora* may be successful in this stressful habitat because its mycorrhizal association meets its energy and nutrient needs making it an obligate mycotroph for most of its existence. As a result, its leaves are reduced (indicating reduced photosynthetic capability), and much of its existence is spent beneath the leaf litter reproducing by means of new tuberoids. Many of *Triphora*'s associates are also saprophytic or root parasites. *Epifagus virginiana* is especially abundant. *Coralorrhiza maculata,* and *Monotropa uniflora* are also found thinly scattered in the herb layer.

Because of the positive correlation with *Fagus grandifolia,* it seems probable that there is a three-way connection from *Triphora* through it's mycorrhizae to the *Fagus* roots and that *Triphora* may be indirectly receiving it's nutrients and photosynthate from the beech trees. A similar situation occurs in the Australian orchid *Gastrodia cunninghamii* which lives almost entirely underground. Its tubers are covered with a network of fungal mycelia which penetrates the living roots of an adjacent tree, most often *Nothofagus* (Withner, 1974). This three-way relationship is known to occur in other orchids and plants (Harley, 1982; Harley and Harley, 1987; Bernhardt, 1989).

Although sample size for tuberoid measurements was small due to the invasive nature of sampling, analysis of the data indicates that the plant's reproductive status depends in part on primary tuberoid size. Since the variability in primary tuberoid size was quite large for 1 to 4 flowered plants and the fact that many

primary tuberoids of flowering size (i.e., greater than .7 cm) were discovered in the litter near measured plants suggests that *Triphora* continues a productive life under the litter reproducing vegetatively after it has produced a flowering shoot. Additional data may show that a primary tuberoid may produce many flowering shoots years apart.

It is not unusual for deciduous forest herbs to reproduce vegetatively as well as by seed. However, even for species that replace themselves primarily vegetatively, seeds are necessary for the establishment of new populations and nearly all species flower (Bierzychudek, 1982). The number of seedpods actually formed relative to the number of flowers produced may be largely controlled by pollinator activity and by general environmental and physiological conditions (Withner, 1974). This limitation of reproductive output by pollinators seems to be a common phenomenon in many species (Bierzychudek, 1981).

From personal observations, the woods in August have few pollinating insects. In order to ensure pollination, many of *Triphora*'s associates remain in flower for an extended time, such as *Solidago caesia, Aster divaricatus,* and *Laportea canadensis. Impatiens pallida* flowers continually throughout the summer with the later flowers being cleistogamous. *Epifagus virginiana,* an abundant saprophyte in the area, has sterile upper flowers, but abundantly fertile cleistogamous lower flowers.

Two other members of the Orchidaceae found scattered over the site include *Epipactis helleborine* and *Corallorhiza maculata.* These both share the feature of long flower availability to pollinators by successive opening of long-lived flowers. *Triphora,* on the other hand, only opens its flowers for one day, and that fact coupled with low pollinator availability accounts for the low capsule set. To offset the short duration of flower availability, however, *Triphora* flowers gregariously, i.e., many flowers open on the same day. Gregarious flowering is obviously an advantage to plants with short-lived flowers, as it gives a much greater chance of pollination than would be the case if the flowers opened sporadically over a long period (Lawson, 1966). These massed floral displays presumably increase the attractiveness to pollinators and in *Isotria verticillata,* the larger clones did have higher pollination percentages (Merhoff, 1983).

Triphora trianthophora appears well adapted to the habitat in which it is found. Since pollination and seed ripening occur rarely, *Triphora* utilizes vegetative propagation by secondary tuberoids

to ensure future generations in the extant population. This type of adaptation, however, may result in a loss of genetic variability in the population, and can become detrimental in that *Triphora trianthophora,* like many other plants, is sensitive to changes in it's habitat. Loss of it's habitat would mean certain destruction for an entire population. The fact that it may not be detected for years at a time makes this unique orchid especially difficult to protect.

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40 DEMERITT AVE.

LEE, NEW HAMPSHIRE 03824

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CALCAREOUS FENS OF WESTERN NEW ENGLAND AND ADJACENT NEW YORK STATE

GLENN MOTZKIN

ABSTRACT

This study presents a community characterization of calcareous fens of western New England and adjacent New York State. Based on analyses of data from 24 sites, seven vegetation types are defined: *Carex lasiocarpa-Cladium mariscoides* Type, *Carex aquatilis* Type, *Betula pumila* Type, *Carex lacustris* Type, *Carex stricta* Type, *Typha angustifolia-Carex lasiocarpa* Type, and *Carex interior-Carex leptalea-Carex flava* Type. The distribution of these vegetation associations is related to hydrologic and ionic gradients. Calcareous fens of the region are similar to minerotrophically rich fens elsewhere in North America with respect to vegetation and environmental characteristics.

Key Words: wetlands, calcareous fens, vegetation classification, ordination

INTRODUCTION

Calcareous wetlands are ecologically significant communities that support numerous rare or uncommon plant species as well as several unusual animal species (McVaugh, 1957; Bernard et al., 1983; Rawinski and Rooney, 1989; Weatherbee, 1990). Historically limited in distribution and extent throughout the northeastern United States, modern development pressure continues to threaten the integrity of several sites.

Although calcareous wetlands are recognized as priorities for conservation, most previous investigations of freshwater wetlands in the northeastern United States have focused on peatlands characterized by acidic, nutrient-poor surface waters (Moizuk and Livingston, 1966; Hemond, 1980; Damman and French, 1987; among others). This research trend reflects the predominance of acidic bedrock throughout the region and has resulted in the general absence of information concerning the vegetation and environmental characteristics of circumneutral to alkaline wetlands. The present study marks the first comprehensive evaluation of calcareous fens in western New England and adjacent New York State, providing baseline information that is critical for conservation and management planning, as well as for future more detailed studies of these communities. The specific objectives of this study are to: 1) characterize vegetation associations of calcareous fens in western New England and adjacent New York

State, 2) relate variation in fen vegetation to environmental parameters, and 3) compare fens of the northeastern United States with those described from elsewhere in North America.

Calcareous fens are non-forested wetlands that are influenced by base-rich groundwater and contain calcicoles (Rawinski, 1984). In the present study, the term 'fen' is applied to both level and sloping communities with or without peat deposits. Although most studies of fens in North America have been restricted to peatlands (Schwintzer, 1978; Slack et al., 1980; Sims et al., 1982; Davis and Anderson, 1991), several European investigators have recognized the floristic and functional similarities between sites with peat and those that lack organic sediments (Wheeler, 1980; Boyer and Wheeler, 1989; Peterson, 1989).

STUDY AREA

In western New England and adjacent New York State, calcareous fens occur primarily as small communities (<1–50 ha) throughout the Berkshire Valley Lowland and portions of the adjacent Taconic Region where carbonate bedrock or surficial deposits occur (Figure 1). Many calcareous fens in the region occur on rocks of the Stockbridge formation, which consist primarily of marble, limestone, dolostone and other carbonate-rich rock types (Motts and O'Brien, 1981). A few fens overlie the Walloomsac and related formations that contain limestone interbedded with schists. A single fen in the Connecticut Valley of Massachusetts occurs on Mesozoic sedimentary bedrock. Although most fens occur on calcareous till deposits, several have developed on glaciofluvial or glaciolacustrine deposits.

Calcareous fens in the region occur at elevations that range from 75 to 400 m a.s.l., with most sites between 150–300 m. Climate throughout the region is continental, with cool winters and warm summers (U.S.D.A., 1988). Average annual precipitation of 110 cm is fairly evenly distributed throughout the year.

METHODS

The methods for this investigation are modified from those established for prior surveys for the Massachusetts Natural Her-

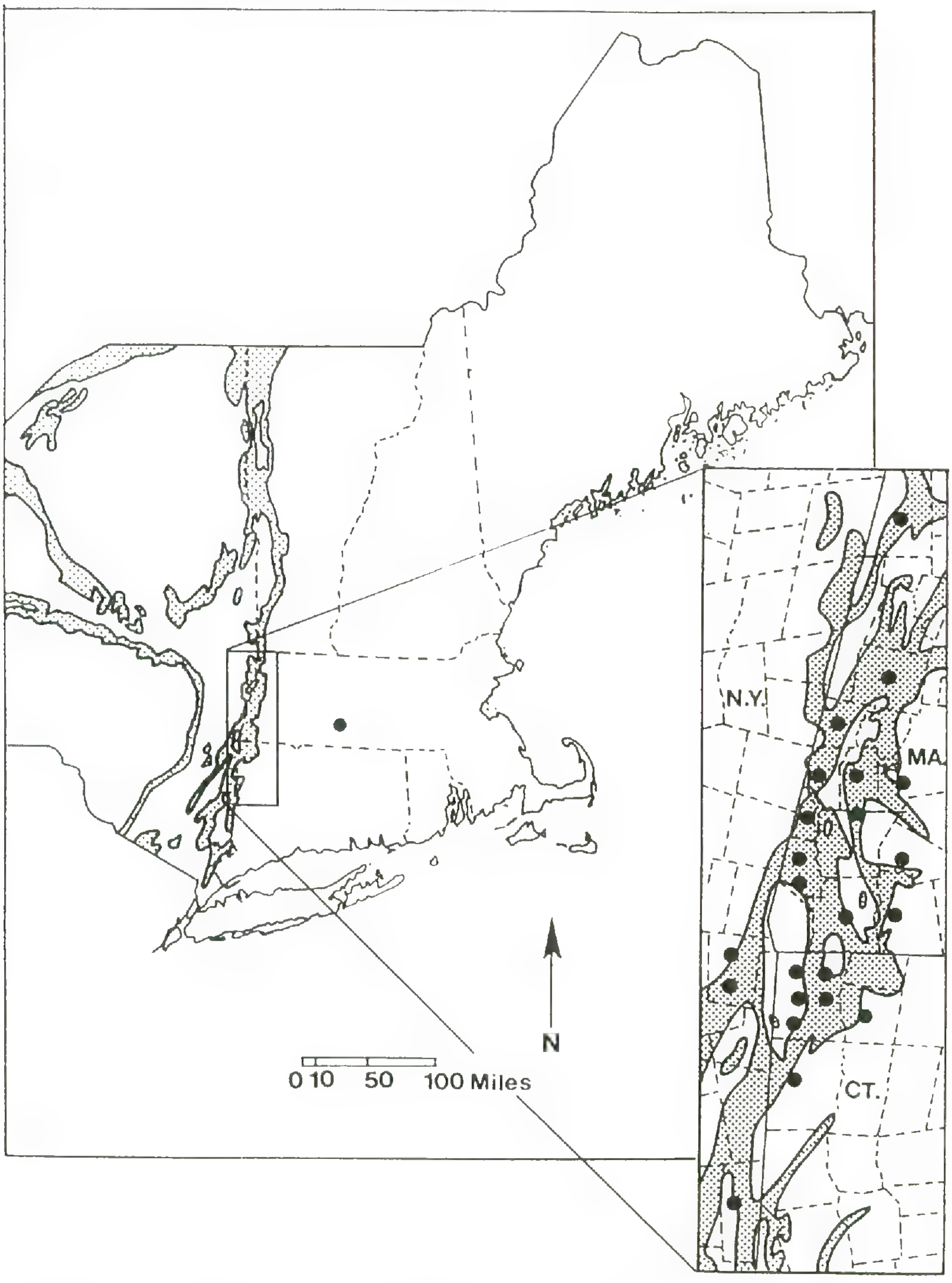

Figure 1. Map showing the location of the study area and the occurrence of carbonate bedrock (stippled) in the northeastern United States. Study sites are indicated as dots on the enlarged inset (right), except for one site in the Connecticut Valley that is indicated on the regional map (left). Modified from Moore (1935), Denny (1982), and Isachsen et al. (1991).

itage and Endangered Species Program (Motzkin, 1991). Field sites were selected in consultation with the staffs of the MA, CT, and NY Natural Heritage Programs and the Eastern Heritage Task Force of The Nature Conservancy. Twenty-four sites, believed to represent most of the undisturbed, non-forested fens in the region, were sampled for vegetation and environmental characteristics.

Fifty-five 100 m^2 relevés (Mueller-Dombois and Ellenberg, 1974) were sampled for vascular plant species-cover estimated within height strata and percent cover of dominant bryophytes. Relevés were subjectively located in areas of uniform vegetation and distributed to encompass a range of vegetation types. General observations of vegetation structure, landform type, site condition, disturbance history, and presence of rare species were also recorded. Bryophytes and unidentified herbaceous species were collected for identification. Nomenclature follows Seymour (1989) for vascular plants, except for *Carex* section Stellulatae, which follows Reznicek and Ball (1980), and *Carex stricta* complex, which follows Standley (1987). Nomenclature for bryophytes follows Crum (1976).

Surface water pH and conductivity were measured at each relevé location. Water samples were collected, refrigerated, and later analyzed at the University of Massachusetts using an atomic absorption spectrophotometer to determine concentrations of calcium, magnesium, and phosphorus. Water color of filtered samples (related to concentration of humic acids) was estimated in three classes: 'clear', 'moderate', or 'dark'. Depth of organic sediments at each relevé was determined by probing to a maximum depth of 2 m. A soil auger was used to determine the degree of decomposition of the upper one meter of organic sediments, estimated according to the Von Post scale (Clymo, 1983).

Relevé cover data were analyzed with cluster analysis and ordination techniques. Agglomerative cluster analysis (AGGLOM; Orloci, 1967) served as the basis for classifying vegetation types and detrended correspondence analysis (DCA; Hill, 1979) was useful in identifying relationships among relevés. Canonical correspondence analysis (CCA; ter Braak, 1986), correlation analysis, and Duncan's Multiple Range Tests were used to identify environmental factors influencing the distribution of plant communities.

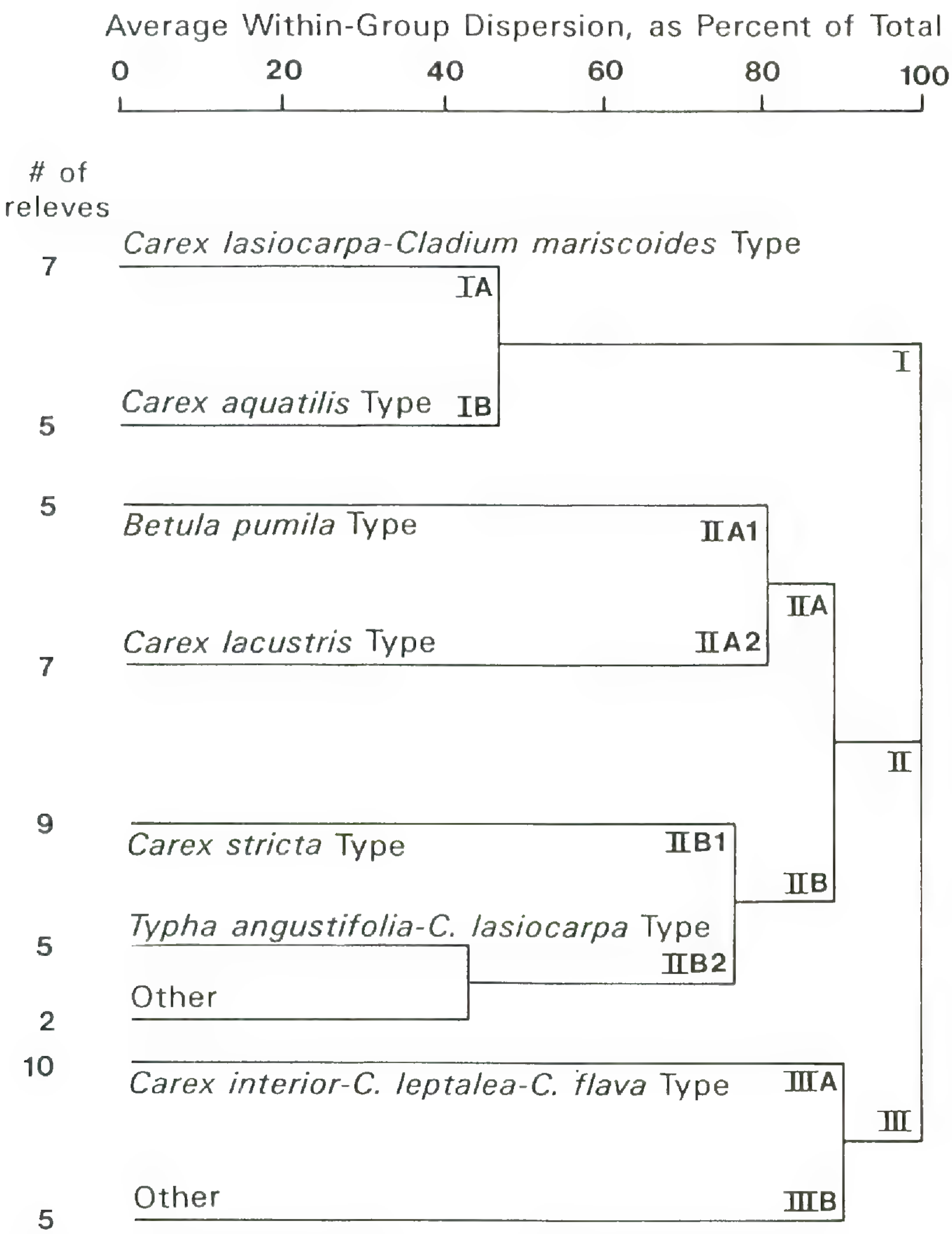

Figure 2. Simplified AGGLOM dendrogram based on absolute distances for species cover in 55 relevés. See text for description of vegetation types.

RESULTS

Vegetation Classification

Relevé data were clustered by AGGLOM using absolute distances into three main groups, composed of several smaller clus-

ters (Figure 2). Group I is characterized by *Carex lasiocarpa, C. aquatilis, Potentilla fruticosa,* and *Myrica gale. Cladium mariscoides, Rhyncospora alba, Sarracenia purpurea, Andromeda glaucophylla, Pogonia ophioglossoides, Drosera rotundifolia, Menyanthes trifolia,* and *Utricularia* spp. occur with greater frequency in this group than in Groups II or III (Table 1). *Sphagnum* spp. and *Campylium stellatum* are the common bryophytes. Uncommon species associated with Group I include *Carex limosa, C. aquatilis,* and others.

Group II is characterized by *Betula pumila, Carex lacustris, C. stricta, Thelypteris palustris, Salix candida,* other *Salix* species, and *Spiraea latifolia. Rhus vernix, Phragmites communis, Typha angustifolia, T. latifolia, Lythrum salicaria,* and *Lysimachia thyrsiflora* are also characteristic of this group. *Galium labradoricum, Betula pumila,* and *Salix candida* are species characteristic of Group II that are regionally uncommon.

Group III is characterized by *Carex interior, C. leptalea, C. flava, C. hystericina, Larix laricina, Parnassia glauca, Solidago patula, S. purshii,* and *Thelypteris palustris,* with *Rhamnus alnifolia, Equisetum fluviatile, Equisetum* spp., *Ribes* spp., and *Cornus* spp. also important. Rare species include *Carex sterilis, C. tetanica, Equisetum scirpoides, Petasites palmatus, Lobelia kalmii,* and *Spiranthes romanzoffiana.*

Within the classification hierarchy, subgroups are characterized by a subset of the species listed for the major groups as well as by additional species. Subgroups that are distinct with respect to species composition and abundance may be considered separate vegetation types (Table 1). Group I includes two such subgroups. The ***Carex lasiocarpa-Cladium mariscoides*** **Type** (Subgroup IA) is a sedge-dominated association characterized by *Carex lasiocarpa, Myrica gale, Potentilla fruticosa, Peltandra virginica,* and *Cladium mariscoides.* Other frequent species include *Drosera rotundifolia, Sarracenia purpurea, Hypericum virginicum, Rhyncospora alba, Typha* species, *Vaccinium macrocarpon,* and *Utricularia* spp. The dominant bryophytes are *Campylium stellatum, Calliergonella* sp., and *Sphagnum* spp.

The ***Carex aquatilis*** **Type** (Subgroup IB) is structurally similar to Subgroup IA but is dominated by *Carex aquatilis* or by *Carex aquatilis* and *C. lasiocarpa* and lacks species such as *Peltandra virginica* and *Hypericum virginicum.*

Group II includes four subgroups. The ***Betula pumila*** **Type** (Subgroup IIA1) is characterized by a shrub layer of *Betula pumi-*

Table 1. Percent frequency of occurrence by Group and Subgroup. * = incomplete sampling of minor bryophytes; no frequencies calculated.

Group:	I		II				III
Subgroup:	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
Trees							
Chamaecyparis thyoides	14						
Acer rubrum	14	20	100	14	57	40	40
Fraxinus spp.			20		29		20
Pinus strobus					14		70
Larix laricina			20				40
Tsuga canadensis							30
Betula alleghaniensis					14		20
Carpinus caroliniana					14		20
Populus tremuloides							20
Quercus alba							20
Betula papyrifera							10
Tilia americana							10
Shrubs							
Chamaedaphne calyculata	14						
Lonicera villosa	14						
Aronia arbutifolia	14					20	10
Andromeda glaucophylla	14	40					
Myrica gale	86	100	40		14	40	
Potentilla fruticosa	86	100	100	71	43	20	80
Alnus spp.	43	40	40	14	86	60	20
Salix discolor	14	20	40	71	14		40
Spiraea latifolia	14		40	43	71	60	40
Cornus stolonifera	14		80	14		40	50
Cephalanthus occidentalis	14		20	14	14	60	
Salix candida		20	20	57	14	80	10
Betula pumila		60	100			40	
Rhus vernix			40	14	14	20	20
Rhamnus alnifolia			20	14			40
Ribes spp.			20	14			60
Salix serissima			40	43	14		50
Salix spp.			60	14	43	20	60
Rosa palustris			40		29		10
Viburnum recognitum			20		14	20	10
Rhamnus frangula			20				
Ilex verticillata	20						
Myrica pensylvanica	20						
Cornus amomum		29	14				
Cornus racemosa		14	14			20	
Spiraea tomentosa			14			10	
Lyonia ligustrina			14			40	
Lindera benzoin			14			20	
Amelanchier sp.			14			20	

Table 1. Continued.

Group:	I		II				III
Subgroup:	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
Vaccinium corymbosum						20	10
Viburnum lentago							30
Corylus spp.							10
Ulmus sp.							10
Vaccinium angustifolium							10
Hamamelis virginiana							10
Rhamnus cathartica							10
Graminoids							
Rhyncospora alba	43						10
Eriophorum gracile	14						
Scirpus acutus	43	20		14		20	
Scirpus hudsonianus	14	40					
Cladium mariscoides	86	60					
Carex lasiocarpa	100	60			14	100	
Carex aquatilis	14	100	40			20	
Phragmites communis		20	40			40	
Carex limosa		20					
Carex prairea		20	40	14	14	40	10
Calamagrostis canadensis			60	57	29	20	10
Poa palustris	14		20				
Carex lacustris			80	100		40	10
Eleocharis erythropoda		20	20	43			20
Carex stricta			40	57	100	60	20
Carex stipata					57		
Scirpus atrovirens					43		30
Carex vulpinoidea					29		
Dulichium arundinaceum						60	
Eleocharis sp.	29	40			14	60	30
Carex comosa			20	14	14	20	
Carex interior			60	29	14		100
Carex leptalea			40	29			100
Carex flava		20	40		29	40	90
Carex hystericina				29	43		80
Carex tetanica			20				30
Eriophorum viridi-carinatum	14				14		50
Glyceria striata			20	43		20	50
Juncus sp.				14	14	20	20
Muhlenbergia glomerata	14		20	14	14		50
Carex scoparia				14	14		
Phalaris arundinacea				14			
Bromus ciliatus			20		14		30
Juncus dudleyi					14		30
Juncus effusus					14		20

Table 1. Continued.

Group:	I		II				III
Subgroup:	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
Juncus nodosus					14		50
Eleocharis acicularis					14		
Leersia oryzoides					14		
Carex rostrata					14		
Poa pratensis					29		10
Carex granularis							40
Anthoxanthum odoratum							20
Festuca spp.							20
Poa compressa							10
Sphenopholis sp.							10
Carex gracillima							10
Carex laevivaginata							10
Carex spp.	14						10
Andropogon scoparius							10
Danthonia spicata							10
Herbs							
Utricularia spp.	29						
Potamogeton spp.	29						
Potentilla palustris	29		40				
Peltandra virginica	71		40		14	40	
Pogonia ophioglossoides	29	20					10
Drosera rotundifolia	86	20				20	50
Sarracenia purpurea	100	80					
Vaccinium macrocarpon	100	80	20				
Menyanthes trifolia	86	100	20			20	
Utricularia intermedia	57	80	20		14		
Typha latifolia	14	60	60	57	14		10
Equisetum fluviatile			100	43	14	40	
Lysimachia thyrsiflora			100	14		40	10
Osmunda regalis	14		40	14			10
Sagittaria latifolia			40		14	20	
Parthenocissus quinquefolia			20		14		
Rubus spp.			80	29	29		40
Polygonum sp.			20	29	29		
Acorus calamus				29			10
Lemnaceae spp.				14	14		
Galium labradoricum			40	43	14		10
Iris versicolor			40	57	14	40	20
Impatiens capensis			20	14	43		
Viola sp.			20		19		
Brasenia schreberi					29		
Solidago spp.			40		14		20
Typha angustifolia	43		40	14	29	100	

Table 1. Continued.

Group:	I		II				III
Subgroup:	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
Thelypteris palustris	29		100	86	71	100	90
Hypericum virginicum	71		20	14	57	80	
Lythrum salicaria			60	14	29	60	20
Eupatorium maculatum			40	43	43		40
Onoclea sensibilis			20	14	29	20	20
Eupatorium perfoliatum				14	14	20	20
Aesclepias incarnata			20	29		40	
Proserpinaca palustris			20	14		20	
Campanula aparinoides					29	40	
Solidago patula					43	20	90
Utricularia minor			20				
Equisetum spp.				14	14		80
Parnassia glauca				43			80
Solidago purshii	14	20	20	43			70
Symplocarpus foetidus			40	43	14	20	50
Thalictrum polygamum			40	14			40
Solanum dulcamara			20	14			
Galium spp.				29	43		40
Rumex spp.				29	14		
Ludwigia palustris				14	14		
Verbena hastata	14						
Umbelliferae spp.	29						10
Hydrocotyl americana					14		40
Achillea millefolium					14		20
Compositae spp.					29		20
Lonicera spp.					14		20
Lysimachia ciliata					14		10
Apios americana					14		10
Nuphar variegatum					14		
Boehmeria cylindrica					14		
Desmodium sp.					14		
Geum rivale							40
Senecio aureus							40
Prunella vulgaris							30
Petasites palmatus							20
Smilacina stellata							20
Potentilla simplex							20
Fragaria sp.							20
Eupatorium rugosum							10
Tussilago farfara							10
Amphicarpa bracteata							10
Geranium maculatum							10
Houstonia sp.							10
Cardamine sp.							10

Table 1. Continued.

Group:	I		II				III
Subgroup:	IA	IB	IIA1	IIA2	IIB1	IIB2A	IIIA
Sanicula marilandica							10
Spiranthes romanzoffiana							10
Taraxacum officinale							10
Chrysanthemum leucanthemum							10
Clematis spp.							10
Cypripedium reginae							10
Adiantum pedatum							10
Aster puniceus							10
Aster schreberi							10
Aster umbellatus							10
Dryopteris cristata							10
Epilobium leptophyllum	14						10
Equisetum scirpoides							10
Lycopus uniflora							10
Lysimachia terrestris						20	10
Mentha arvensis							
Unknown	14		20	14	29		20
Bryophytes							
Sphagnum fimbriatum	14						
Sphagnum subsecundum var. *contortum*	14						
Drepanocladus sp.	14		20	14		60	
Calliergonella sp.	71	40	60	14	14	40	10
Campylium stellatum	86	100	80	57	29	40	60
Sphagnum warnstorfii	14						30
Sphagnum spp.							20
Sphagnum magellanicum							10
Thuidium delicatulum			*				
Leptodictyum sp.					*		
Aulacomnium palustre							*
Cratoneuron filicinum							*
Scorpidium scorpioides							*
Tomenthypnum nitens							*
Helodium blandowii							*
Dicranum scoparium							*
Thuidium recognitum							*

la, Potentilla fruticosa, Acer rubrum, Cornus stolonifera, and *Salix* spp., amidst herbaceous species such as *Carex lacustris, Calamagrostis canadensis, Typha angustifolia, T. latifolia, Lysimachia thyrsiflora, Lythrum salicaria, Thelypteris palustris, Equisetum*

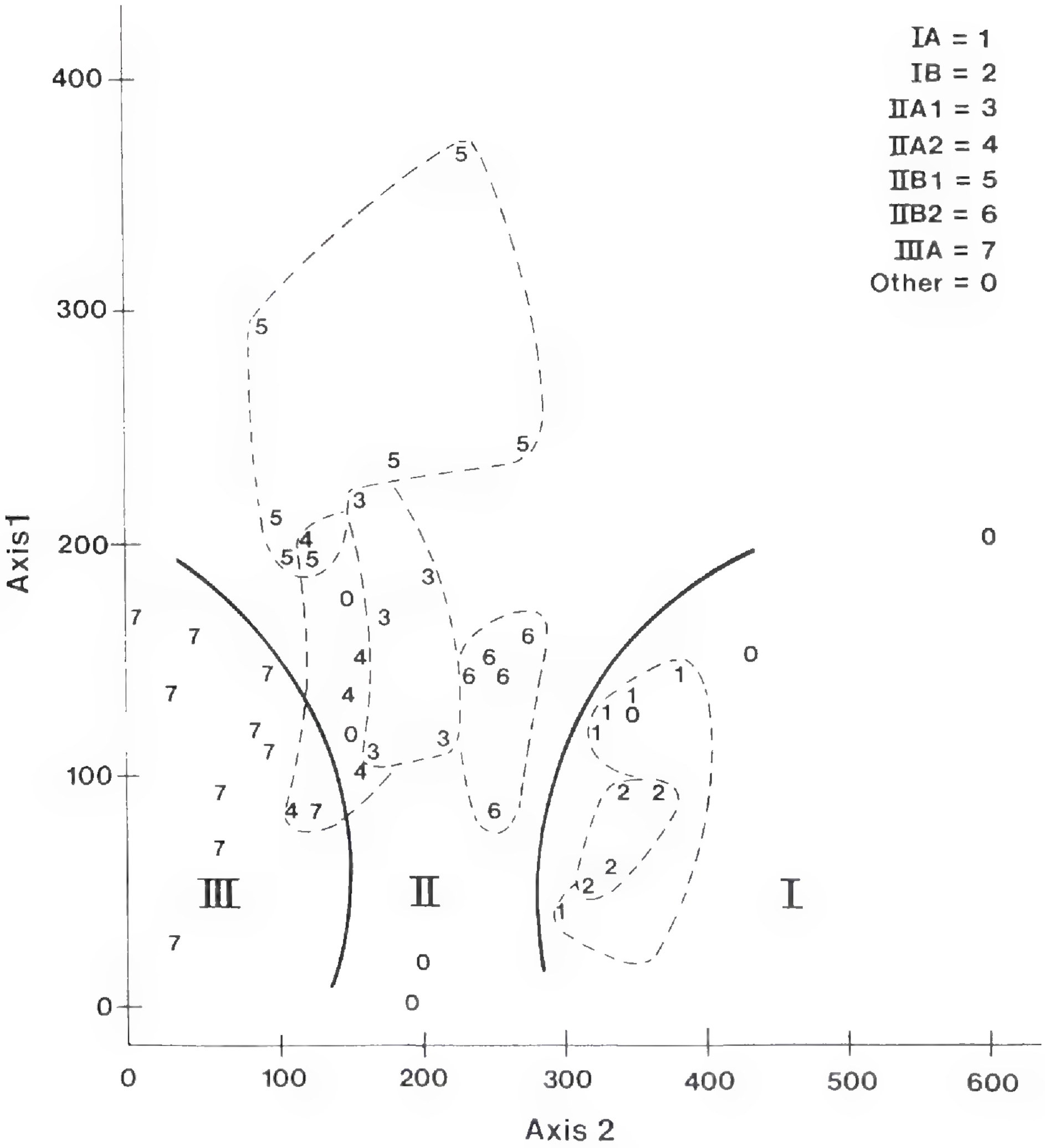

Figure 3. Plot of DCA sample ordination for axes 1 and 2. Numbers refer to groups and subgroups defined by cluster analysis (Figure 2).

fluviatile, and *Campylium stellatum. Rhus vernix* is locally abundant.

The ***Carex lacustris*** **Type** (Subgroup IIA2) includes some of the species found in the *Betula pumila* type, but lacks extensive woody cover. Frequent species include *Carex lacustris, C. stricta, Salix candida, Potentilla fruticosa, Typha* spp., and *Thelypteris palustris.*

The ***Carex stricta*** **Type** (Subgroup IIB1) has higher frequency and cover values for *Carex stricta* than other subgroups. *Acer*

rubrum, Alnus sp., *Scirpus atrovirens, Galium* spp., *Eupatorium maculatum,* and *Thelypteris palustris* are other characteristic species.

The ***Typha angustifolia-Carex lasiocarpa*** **Type** (Subgroup IIB2) is dominated by *Typha angustifolia* and *Carex lasiocarpa,* with *Salix candida, Cephalanthus occidentalis, Dulichium arundinaceum, Eleocharis* spp., *Campanula aparinoides,* and *Hypericum virginicum* frequently encountered. *Potentilla fruticosa* is less frequent in this subgroup than in any other vegetation type identified through cluster analysis. Two plots in this Subgroup are shown as 'Other' in Figure 2. These plots are dominated by *Scirpus acutus* with only low cover of species characteristic of the *Typha angustifolia-Carex lasiocarpa* Type.

Group III includes two subgroups. The ***Carex interior-C. leptalea-C. flava*** **Type** (Subgroup IIIA) has sparse tree and shrub strata containing *Pinus strobus, Larix laricina, Potentilla fruticosa, Salix serissima, Ribes* spp., and *Rhamnus alnifolia,* and a low herbaceous stratum characterized by *Carex interior, C. leptalea, C. flava, C. hystericina, Juncus dudleyi, J. nodosus, Muhlenbergia glomerata, Parnassia glauca, Solidago purshii,* and *S. patula.* Relevés in Subgroup IIIB are shown as 'Other' in Figure 2 because these plots contain vegetation that appears transitional between two or more of the types described above.

Figure 3 presents the results of the DCA ordination, with relevés assigned according to the groups and subgroups defined by cluster analysis. The grouping of relevés along the ordination axes demonstrates the lack of overlap between types defined by cluster analysis at both a coarse (major groups) and fine level (subgroups) of classification.

Environmental Characteristics

The surface waters of the calcareous fens investigated are circumneutral to alkaline (pH: 6.0–8.1), with relatively high concentrations of calcium (8–65 mg/liter) and magnesium (4–32 mg/liter) (Table 2). Phosphorus levels are low, with only 8 out of 55 samples above the detection limit of .15 ppm (not shown in Table 2). Depth of organic sediments range from >200 cm in most Group I sites to 0–15 cm in areas with visible groundwater seepage (Group III). Where organic sediments occur, the degree of de-

Table 2. Environmental characteristics of calcareous fens of western New England and adjacent New York State (average value with range in parentheses). Groups and vegetation types numbered as in Figure 3. Color refers to filtered samples (1 = clear, 2 = moderate, 3 = dark).

	No. of Samples	pH	Conductivity (μmho)	CA (mg/liter)	MG (mg/liter)	Depth* (cm)	Von Post (0–10)	Color (1–3)
Group I	12	6.6 (6.0–7.1)	415 (87–1151)	31 (11–62)	10 (4–17)	200	3 (2–3)	2 (1–3)
Type 1	7	6.5 (6.0–7.0)	213 (87–322)	22 (11–34)	10 (4–17)	200	3 (3–3)	2 (1–3)
Type 2	5	6.8 (6.5–7.1)	697 (225–1151)	43 (26–62)	10 (7–14)	200	3 (2–3)	2 (1–3)
Group II	26	6.9 (6.5–7.7)	366 (208–581)	43 (8–65)	19 (7–32)	135 (20–200)	7 (3–9)	2 (1–3)
Type 3	5	6.8 (6.7–6.8)	391 (251–505)	43 (34–52)	19 (11–26)	171 (55–200)	5 (3–8)	2 (1–2)
Type 4	7	6.8 (6.5–7.4)	341 (225–461)	50 (30–62)	16 (10–22)	141 (65–200)	7 (3–9)	1 (1–3)
Type 5	9	7.1 (6.7–7.7)	371 (248–515)	45 (16–65)	19 (7–32)	103 (20–200)	8 (3–9)	2 (1–3)
Type 6	5	6.9 (6.7–7.2)	368 (208–581)	35 (8–50)	22 (15–29)	150 (75–200)	5 (3–9)	1 (1–2)
Group III	10	7.2 (6.9–8.1)	333 (158–478)	46 (26–62)	17 (8–23)	20 (0–70)	7 (3–9)	1 (1–2)
Type 7	10	7.2 (6.9–8.1)	333 (158–478)	46 (26–62)	17 (8–23)	20 (0–70)	7 (3–9)	1 (1–2)

* Maximum value of 200 cm.

composition within the uppermost one meter of sediments varies from largely undecomposed peat (Von Post scale: 2–3) in many Group I plots, to highly decomposed muck (Von Post: 7–9) in Group II sites.

Correlation analyses indicate a significant negative relationship between depth of organic sediments and pH ($R = -.63$; $P = .0001$), degree of decomposition ($R = -.45$; $P = .0017$), and Mg concentration ($R = -.33$; $P = .02$). Ca concentration is positively correlated with Mg concentration ($R = .58$; $P = .0001$), and with conductivity ($R = .49$; $P = .0004$), and both Ca and Mg are negatively correlated with hydrogen ion concentration (Ca: $R = -.39$, $P = .01$; Mg: $R = -.39$, $P = .01$). pH is positively correlated with degree of decomposition of peat ($R = .34$; $P = .03$). Water color is positively correlated with hydrogen ion concentration ($R = .36$; $P = .01$).

Relationship Between Vegetation and Environment

Canonical correspondence analysis (CCA; ter Braak, 1986), a form of direct gradient analysis in which the vegetation ordination is constrained by environmental data, was used to relate vegetation variability to measured environmental variables. In the resulting ordination (Figure 4), relevés separate primarily along gradients of depth of organic sediments, pH, and degree of decomposition of organics. Ca, Mg, conductivity, and water color account for less of the variability in the vegetation. Combined, these environmental factors account for a relatively low percentage of the total variability of the vegetation (~25%), reflecting the fact that the fens investigated are highly variable with respect to vegetation and water chemistry. ter Braak (1986) has noted this pattern for other data sets, suggesting that CCA may still be useful in cases where a relatively low percentage of the total variability is accounted for by the ordination diagram.

The hierarchical nature of cluster analysis allows one to test the hypothesis that different environmental variables are associated with vegetation variation at different levels of classification. For example, in montane systems one might hypothesize that elevation gradients are responsible for patterns of vegetation variation at a coarse level. Within a particular elevation zone, however, local edaphic factors (rather than elevation) might control patterns of vegetation variation. Duncan's Multiple Range Tests

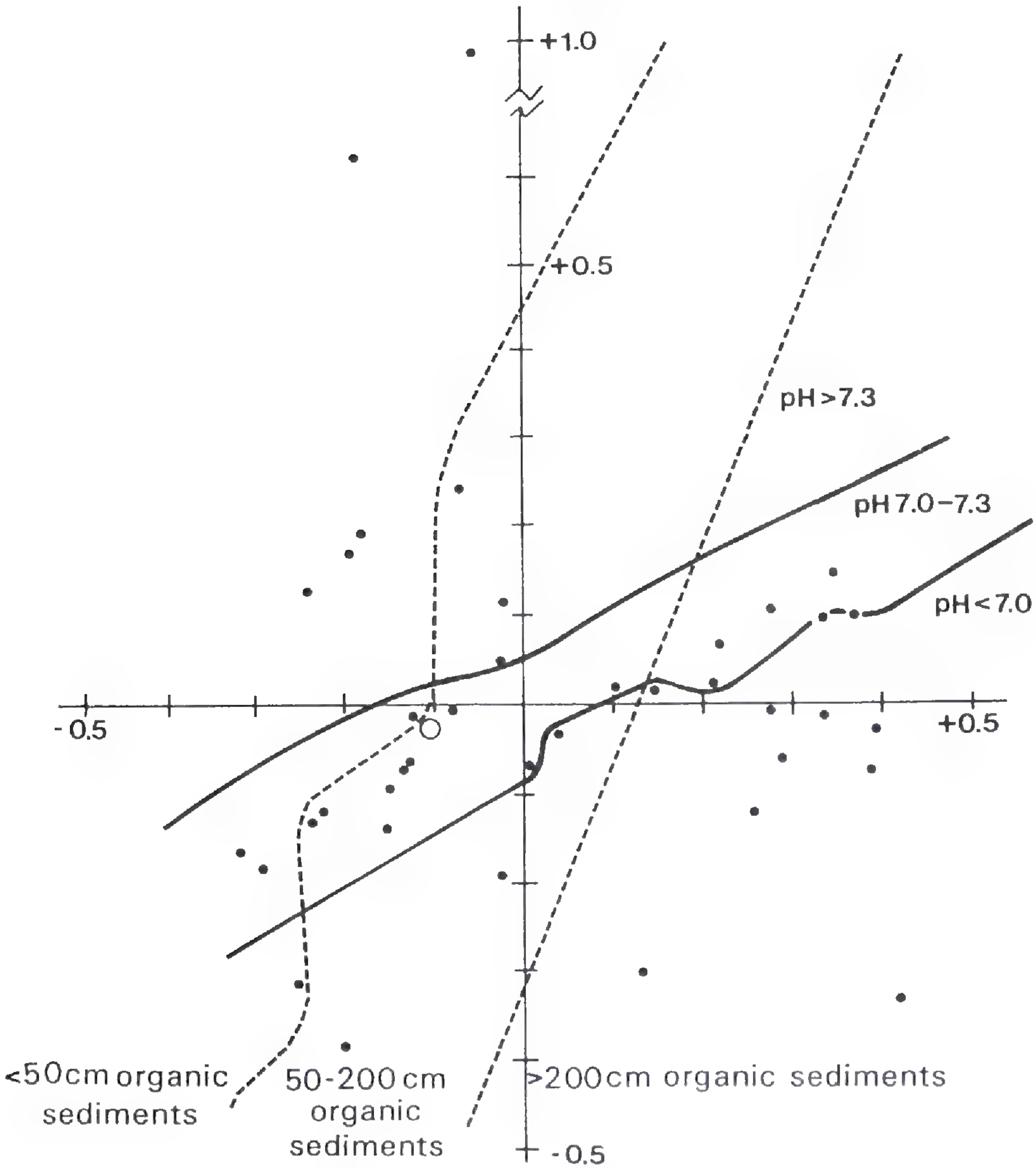

Figure 4. Plot of CCA sample ordination for axes 1 and 2. Broken lines distinguish plots with >200 cm, 50–200 cm, and <50 cm of organic sediments. Solid wavy lines separate plots with pH values of >7.3, 7.0–7.3, and <7.0. An outlier with respect to pH class (pH = 7.4) is indicated by an open circle.

were used to determine which environmental factors differ significantly with respect to major vegetation groups and subgroups defined by cluster analysis.

At the coarse level of classification, depth to mineral soil is the only variable measured that differs significantly ($P = .0001$) between all three groups. Hydrogen ion concentration, Mg, and degree of decomposition of organics (Von Post value) for Group

I are significantly different ($P = .01$, $P = .0004$ and $P = .0001$, respectively) from Groups II and III (which are not different from each other). Calcium levels are different ($P = .07$) between Groups I and III, but not between Groups I and II or between Groups II and III. Conductivity and color of filtered samples do not vary significantly among the three groups. These results suggest that Groups I and III (defined by cluster analysis of relevé data) are most different with respect to environmental parameters (e.g., depth of sediments, pH, Mg, degree of decomposition, and Ca) and that Group II is intermediate with respect to these variables. As with the CCA results, depth to mineral soil is the single variable most strongly associated with vegetation patterns at this level of classification.

Similar analyses were performed to determine environmental differences between subgroups within each major cluster group. Within Group I, Subgroup 1A differs significantly from Subgroup 1B with respect to Ca concentration ($P = .0223$) and conductivity ($P = .0098$). Within Group II, only Von Post values differ between the subgroups ($P = .0767$), with Subgroup IIB1 significantly different from Subgroup IIA1 (but not from IIA2 and IIB2), and Subgroups IIA1, IIA2, and IIB2 not significantly different from each other. No other environmental parameters tested differ significantly between subgroups defined by cluster analysis. Group III contains only one subgroup (IIIA) considered to be a distinct vegetation type, and so was not included in this level of analysis.

DISCUSSION

Relationship of Vegetation to other North American Fens

The coarse level of classification determined through cluster analysis of relevé data can be related to existing classifications of calcareous wetlands. Group I corresponds to a Lake Basin Graminoid Fen type described from the Northeast (Rawinski, 1984; Weatherbee, 1990), and to a Rich Graminoid Fen type of New York State (Reschke, 1990). Dominant species in this group are also recorded from minerotrophic fens of northern Michigan (Schwintzer, 1978). Group II contains elements of the Seepage Swamps of highly calcareous soils described by McVaugh (1957)

and the Seepage Marsh of Rawinski (1984), which he describes as having characteristics of both fen and marsh. Rich-fen types from Britain are structurally similar to Group II vegetation (Wheeler, 1980). Group III, which corresponds to Reschke's (1990) Rich Sloping Fen and to Rawinski's (1984) Calcareous Sloping Fen, contains several species considered to be 'rich fen indicator species' in Ontario (e.g., *Carex leptalea, Eriophorum viridi-carinatum, Scorpidium scorpioides*; Sims et al., 1982).

Several of the vegetation types (subgroups) described here are also related to types found elsewhere in North America. The *Carex lasiocarpa-Cladium mariscoides* Type (Subgroup IA) has been described from a Maine peatland (Rawinski and Rooney, 1989). The vascular vegetation of the *Carex aquatilis* Type is apparently related to the *Drepanocladus revolvens-Carex aquatilis* association found in patterned rich fens in western Alberta (Slack et al., 1980), although none of the study sites investigated in our region display the physiographic patterning typical of fens in boreal climates (Foster and King, 1984; Glaser, 1987). Additional work is needed to evaluate the bryophyte composition of this type.

The *Betula pumila* Type corresponds to a 'larch-birch-sumac swamp type' described from a site included in this investigation (McVaugh, 1957) and to the Rich Shrub Fens of New York (Reschke, 1990). The *Carex stricta* Type is apparently similar to the Sedge Meadow communities found in Maine and New York (Reschke, 1990; Gawler, 1991). No published descriptions correspond closely to the *Typha angustifolia-Carex lasiocarpa* Type.

The *Carex interior-C. leptalea-C. flava* Type contains species described by numerous authors as typical of rich calcareous fens (e.g., Sims et al., 1982; Vitt and Chee, 1990), although no specific reference to this association occurs from outside the region.

Field observations suggest that two additional vegetation associations occur in fens of the region but were inadequately sampled in the current study. A *Scirpus acutus* association was observed in several of the largest peatland fens and along marl pond shores. Also, extensive *Phragmites communis*-dominated areas occur in association with several of the vegetation types described above. Additional sampling is required to relate these associations to the vegetation classification presented here and to those developed for other regions of North America.

Environmental Characteristics

Several authors have related vegetation patterns to environmental characteristics of graminoid-dominated peatland fens elsewhere in North America (Schwintzer, 1978; Slack et al., 1980; Sims et al., 1982; Foster and King, 1984; Vitt and Chee, 1990). Comparison of environmental characteristics reported here (Table 2) with those of previous investigations (Table 3) suggests that the groups and subgroups defined in the current study are comparable to minerotrophically rich fens sampled throughout North America. Of the types considered here, Group I is apparently the least 'rich' (with respect to surface water chemistry), Group II sites are intermediate, and Group III may be characterized as extremely rich (Table 2).

Group I represents a peatland-fen type characterized by deep organic sediments, permanently saturated conditions, and consolidated or floating, sedge-dominated organic mats. Although little is known of the developmental history of these fens in our region, preliminary observations of the macrofossil stratigraphy of two sediment cores extracted from Kampoosa Fen in Stockbridge, MA indicate that since the development of a peat mat at this site, fairly uniform sedge and shrub-sedge peat has accumulated to a depth of 270 cm. This suggests that vegetation structurally similar to the modern vegetation has occupied the site since the time of peat mat establishment. Although the time it has taken for these 270 cm of sediments to accumulate is not known, an estimate of a few thousand years seems reasonable, based on estimates of peat accumulation rates from throughout northeastern North America. Thus, the vegetation at this site appears relatively stable and there is no indication of rapid infilling or terrestrialization.

Sites supporting Group II vegetation are characterized by 50–200+ cm of moderate to well-decomposed organic sediments occurring in a variety of seasonally inundated depressions and drainages. Vegetation characteristic of this group occurs in basins that also support Group I vegetation, in canopy gaps within rich forested swamps, in drainages with current or former beaver impoundments, and in level to slightly sloping sites adjacent to Group III vegetation.

Group III sites are slightly to moderately sloping with groundwater seepage frequently visible in distinct rivulets. In areas of

Table 3. Chemical properties of waters from North American wetlands (average values with range in parentheses). From Zoltai (1988).

Wetland Class	No. of Samples	pH	Conductivity (μmho)	CA (mg/liter)	MG (mg/liter)	Source
Bog	18	4.0 (3.7–4.4)	—	2.3 (1.2–3.7)	0.4 (0.2–0.9)	Schwintzer (1981)
	13	(4.6–5.1)	(35–62)	(0.2–0.8)	(0.1–0.2)	Gauthier (1980)
	10	(3.8–4.4)	31	0.2	0.1	Foster and King (1984)
Fen (poor)	193	(4.6–5.2)	(18–59)	(0.4–4.8)	(0.1–0.7)	Gauthier (1980)
	14	(4.7–5.5)	49	0.3	0.2	Foster and King (1984)
	1	5.0	—	2.4	0.4	Vitt et al. (1975)
Fen (moderately poor)	42	5.2	65	1.1	0.2	Gauthier (1980)
Fen (intermediate to rich)	9	7.2 (6.8–7.9)	281 (140–456)	28 (18–37)	11 (4–28)	Slack et al. (1980)
	21	6.1 (5.2–6.9)	59 (33–128)	10 (4–18)	—	Glaser et al. (1981)
	5	6.5 (5.4–7.1)	—	43 (7–124)	10 (2–15)	Schwintzer (1978)
Swamp (coniferous)	12	7.2 (6.9–7.8)	—	40 (22–52)	12 (8–17)	Schwintzer (1981)

heavy groundwater discharge, mineral soil is typically exposed. Elsewhere, small hummocks develop with shallow accumulations of organic matter. Field observations suggest that the importance of woody species in seepage fens is inversely related to disturbance, with more highly disturbed sites (i.e., those that are flooded by beavers, grazed, or mowed) supporting only low, scattered shrubs. A similar pattern has been described from European fens (Regnéll, 1980; Peterson, 1989).

Environmental Gradients and Vegetation Distribution

CCA analyses indicate that depth to mineral soil is the environmental parameter that accounts for the greatest portion of the variability in the relevé data, with degree of decomposition of organics and pH also important. Duncan's Multiple Range Tests also indicate depth as a significant variable, along with degree of decomposition, pH, Ca, and Mg concentrations. In the study sites considered, depth of peat probably reflects a gradient of 'rate of groundwater-flow' ranging from 'slow' (and poorly aerated) in well-defined basins with deep peat accumulations (Group I), to relatively 'rapid' (and well aerated) in sloping (Group III) sites that lack peat. Depth of peat may also indicate the relative availability to vegetation of nutrients or cations derived from contact with mineral soil. The results of both CCA and Duncan's Multiple Range Tests suggest the importance of both hydrologic gradients (as indicated by depth of organic sediments) and ionic gradients related to alkalinity-acidity (pH, Mg, and Ca concentrations) in determining the variability between the rich fen types considered here.

Similar hydrologic and ionic gradients have been related to vegetation distribution in fen types throughout North America. Peat depth, pH, water levels, and water chemistry are related to differences between fens in Canada (Slack et al., 1980; Sims et al., 1982; Vitt and Chee, 1990). Vegetation variation in a peat and marl fen in western New York is related to complex gradients associated with hydrology, soil organic matter, and soil carbonate-carbon concentrations (Bernard et al., 1983). In one of the few detailed studies to consider non-peatland fens, Boyer and Wheeler (1989) suggest that structural and compositional variation in seepage fens in Britain is related to differences in phosphorus availability between high and low groundwater discharge areas.

At a fine level of classification, subgroups within Group II do not differ significantly with respect to most environmental parameters measured. This probably reflects the high degree of variability of the measured environmental parameters, a pattern noted by several authors (e.g., Sims et al., 1982) for rich fens elsewhere in North America.

Within Group I, relevés in the *Carex lasiocarpa-Cladium mariscoides* Type differ significantly from those in the *Carex aquatilis* Type with respect to Ca concentration and conductivity, but not with respect to depth of organics or degree of decomposition. This suggests an ionic (alkalinity-acidity) rather than hydrologic gradient, with the *Carex lasiocarpa-Cladium mariscoides* Type representing the 'poorer' type. This corresponds well with the observation that in the northeastern United States, *Carex lasiocarpa* occurs at sites ranging from poor to rich, whereas *Carex aquatilis* is restricted to minerotrophically rich sites. These results also suggest that with respect to Group I, different environmental gradients (hydrologic vs. minerotrophic) may be associated with vegetation variation at different levels of classification.

CONCLUSIONS

Calcareous fens of western New England and adjacent New York State are similar to rich peatland fens throughout North America with respect to species composition, water chemistry, and the influence of hydrologic and minerotrophic gradients on vegetation distribution. Future attempts to develop regional classifications of fens should more fully evaluate seepage and seasonally inundated types. In cases where hydrologic and ionic (alkalinity-acidity) gradients do not appear to explain observed variability in vegetation, factors such as nutrients, developmental history, response to disturbance, or biotic interactions may be significant.

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HARVARD FOREST
HARVARD UNIVERSITY
PETERSHAM, MASSACHUSETTS 01366

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CHROMOSOME NUMBERS OF SOME LATIN AMERICAN SPECIES OF *ALNUS* (BETULACEAE)

GUILLERMO RESTREPO AND CAMILLE GERVAIS

ABSTRACT

The chromosome numbers of *Alnus acuminata* H.B.K. ssp. *acuminata, A. acuminata* ssp. *arguta* (Schlechtendal) Furlow and *A. jorullensis* H.B.K. ssp. *jorullensis* were determined on material from 10 different localities of 4 Latin American countries: Columbia (6 stations), Venezuela (1), Costa Rica (2) and Guatemala (1). All the species were tetraploid (2n = 28), *A. acuminata* ssp. *arguta* and *A. jorullensis* ssp. *jorullensis* being cytologically studied for the first time.

Key Words: chromosome numbers, tropical highland forest, *Alnus acuminata, Alnus jorullensis,* Columbia, Venezuela, Costa Rica, Guatemala

INTRODUCTION

The present paper is a part of a comprehensive study, initiated in 1990 by the first author, on the genetic variation and ecology of *Alnus acuminata* H.B.K. ssp. *acuminata.* in Columbia.

This species has a large geographical and ecological distribution along the Andes cordillera, from western Venezuela to northern Argentina (Furlow, 1979). In Columbia, *A. acuminata* behaves as a pioneer species whose normal distribution is between 1700 and 3300 m in the Central and the Oriental cordilleras (Del Valle Arango and González Pérez, 1988). According to the classification system of Holdridge (1967), *A. acuminata* is present in the following types of habitats: dry forest-lower montane (df-LM), moist forest-lower montane (mf-LM), wet forest-lower montane (wf-LM), moist forest-montane (mf-M) and wet forest-montane (wf-M).

In the Central cordillera the species presents itself as a tree which can grow up to 40 m high and 70 cm in diameter. In the Oriental cordillera, however, mostly shrubby specimens are observed and only a few trees in certain habitats exceed 10 m.

Because of these phenotypic (or possibly genetic) variations, chromosome counts on some representative individuals of the species in its natural and more septentrional area were carried out. The only previous cytological determinations on Latin American material of this taxon were those of Giusti (1989) from Tucumán, in Argentina, and those of Coba de Gutiérrez and Alvarado de Coral (1989) from Manizales in Columbia. The chromosome number 2n = 28 was reported in both cases. As a

complement to the present chromosomes studies on the typical subspecies (ssp. *acuminata*), additional counts were realized on ssp. *arguta,* from Costa Rica, and on *A. jorullensis* from Guatemala.

The chromosome number 2n = 28 was the only one found in the native species of *Alnus* in Canada and in the United States (Furlow, 1979), though at least five ploidy levels are reported in the genus. Besides the tetraploid level (2n = 28) which is the most common, a diploid species (*A. inocumae* Mur & Kus. = *A. hirsuta* Turkz. var. *microphylla* Kusaka) is indicated for Japan (Chiva, 1962) and many European and Asiatic species have 2n = 42 or 2n = 56 chromosomes (Gram et al., 1941; Chiva, 1966; Furlow, 1979; Hall and Maynard, 1979; Bousquet and Lalonde, 1990). Finally, *A. firma* Sieb. & Zucc. and *A. sieboldiana* Matsum. from Japan are reported to possess 2n = 112 chromosomes (Kodama, 1967, 1970), at least in the root nodule tissues.

A few species are reputed to present two or three polyploidy levels: *A. cordata* and *A. orientalis* Decne. have both 2n = 28 or 42, *A. hirsuta* Turcz. 2n = 28 or 2n = 56, *A. glutinosa* (L.) Gaertn., *A. japonica* Sieb. et Zucc. and *A. subcordata* Mey. 2n = 28, 42, or 56 chromosomes (Gram et al., 1941; Chiva, 1966; Furlow, 1979; Hall and Maynard, 1979; Bousquet and Lalonde, 1990). The chromosome number 2n = 42 could be interpreted as the result of hybridization (Gram et al., 1941; Furlow, 1979).

MATERIAL AND METHODS

Nutlets of *A. acuminata* ssp. *acuminata* from 7 stations (6 from Columbia, one from Venezuela) were collected between June and August, 1990, by the first author. Additional seeds (*A. acuminata* ssp. *arguta* from two stations in Costa Rica and *A. jorullensis* from one provenance in Guatemala) were also received by exchange services.

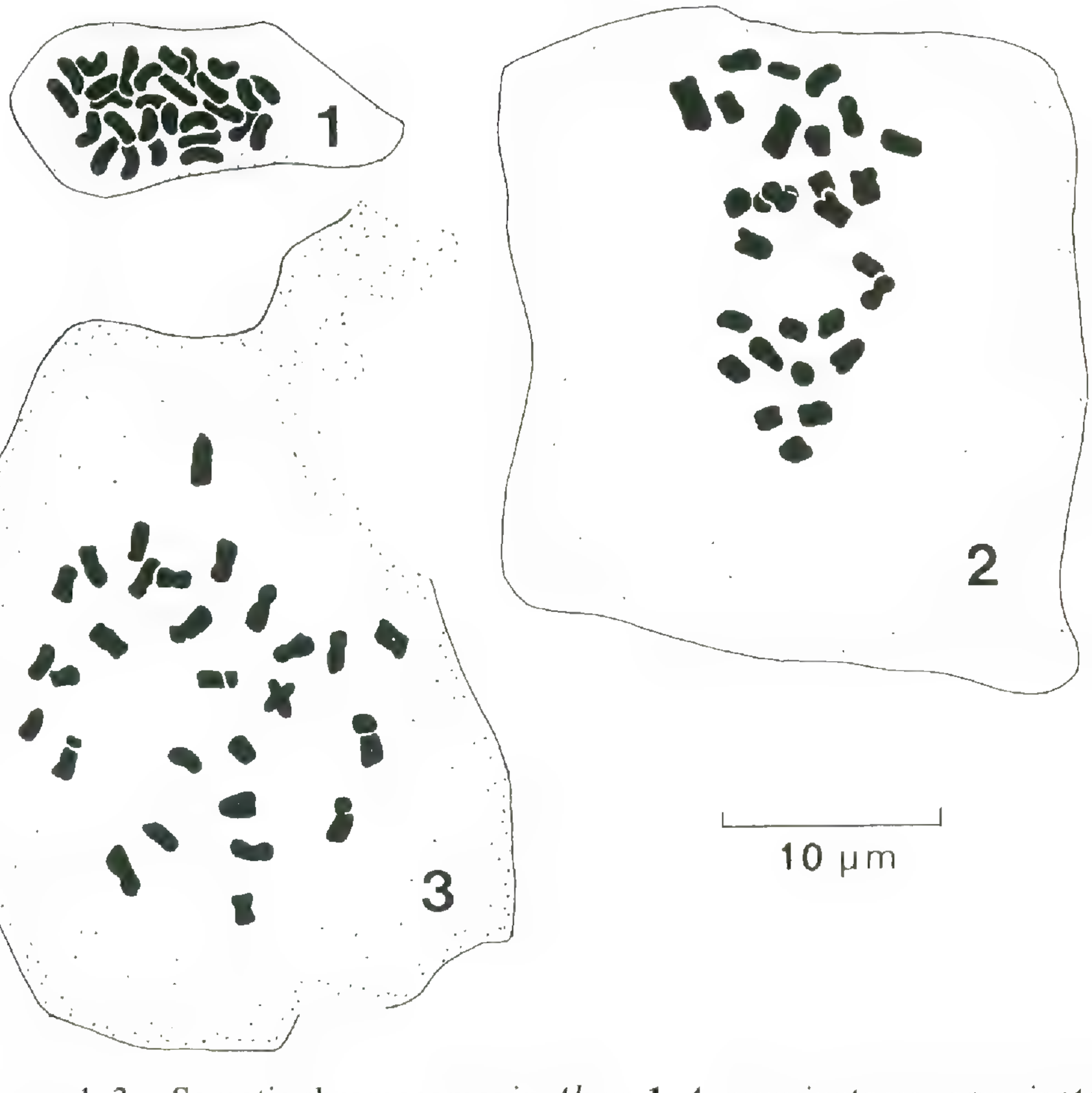
The seeds were sterilized in 6% sodium hypochlorite for 10 minutes, washed in 70% ethanol for 30 seconds and rinsed in sterile distilled water for another 30 seconds. Afterwards they were sown on a 5 mm layer of silica in Petri dishes. The Petri dishes were kept in a germination incubator with a 12 hour photoperiod and 80% humidity. The day temperature was 23°C and the night 18°C.

For the cytological study, seedlings were collected when the first

Table 1. Chromosome counts in *Alnus acuminata* H.B.K. and *A. jorullensis* H.B.K. from Latin America.

Cordillera	Locality	Latitude (N)	Longitude (W)	Altitude (m)	No. of Tree	Chr. Number* (2n)
		A. acuminata H.B.K. ssp. *acuminata*				
		Columbia				
Nudo de Pasto	Santa Lucía, La Cocha (Nariño)	1°03′	77°05′	2710	C18-1	28
Central	Rio Piendamó, Silvia (Cauca)	2°36′	76°21′	2300	C32-5	28
Central	Rio Verde, Pijao (Quindío)	4°20′	75°36′	2290	C07-3	28
Central	Cocora, Salento (Quindío)	4°45′	75°33′	2600	C11-2	28
Central	La Cristalina, Neira (Caldas)	5°21′	75°32′	2380	C02-3	28
Oriental	Rio Pómeca, Arcabuco (Boyacá)	5°44′	73°26′	2790	C30-5	28
		Venezuela				
Oriental	Rio Chama, Tabay (Mérida)	8°38′	71°04′	2050	C27-2	28
		A. acuminata ssp. *arguta* (Schlechtendal) Furlow				
		Costa Rica				
Talamanca	Jardín, Sta. María Dota (Cartago)	9°42′	83°57′	2000	CR-1	28
Volcánica Central	Prusia, Llano Grande (Cartago)	9°56′	83°54′	2200	L125-1	28
		A. jorullensis H.B.K. ssp. *jorullensis*				
		Guatemala				
Tierras Altas	Siguampar (Sacatéquez)	14°35′	90°48′	2000	AJ91-1	28

* The chromosome numbers have been counted from seeds collected *in situ*.



Figures 1–3. Somatic chromosomes in *Alnus*. **1.** *A. acuminata* ssp. *acuminata*; metaphase (2n = 28) in young leaf tissue after cold treatment (7 hr. at 4°C); Arcabuco, Columbia. **2.** *A. acuminata* ssp. *arguta*; metaphase (2n = 28) in root tip tissue after cold treatment of plantlet (7 hr. at 4°C); Santa María de Dota, Costa Rica. **3.** *A. jorullensis* ssp. *jorullensis*; metaphase (2n = 28) in root tip tissue after cold treatment of plantlet (7 hr. at 4°C); Siguampar, Guatemala.

pair of leaves appeared and were deposited in cold water in a refrigerator (4°C) for about 7 hours. This pre-treatment was necessary to shorten the chromosomes before the fixation of the seedlings in a 3:1 mixture of anhydrous alcohol and glacial acetic acid. The root tips or very young leaves were used to count the chromosomes after coloration in acetocarmine for at least 2 hours. The drawings were done with the help of a *camera lucida*.

RESULTS AND DISCUSSION

The chromosome number 2n = 28 was observed for all of the individuals studied in the three taxa (Table 1). This tetraploid

number is actually reported for all of the chromosome counts published for American species of *Alnus* (Furlow, 1979).

In our material, the chromosome being rather small (1.25 to 2.5 μm; Figures 1–3), it was not possible to prepare a karyogramme for any of the species. However, since the chromosomes of *A. jorullensis* ssp. *jorullensis,* showed more details (Figure 3), it could be tentatively assumed that 2 pairs are metacentric, 8 submetacentric, 3 acrocentric and one telocentric.

The chromosome counts for *A. acuminata* ssp. *arguta* and *A. jorullensis* ssp. *jorullensis* are apparently the first reports for these two species. The other taxon, *A. acuminata* ssp. *acuminata,* have been studied in 7 different stations from three cordilleras, one of the stations being in Venezuela and the others in Columbia (Table 1). The station of Neira, in the central cordillera, is not far from Manizales (5°15′N, 75°30′W) where the chromosome number of *A. acuminata* was earlier reported by Coba de Gutiérrez and Alvarado de Coral (1989). It could be noted that the chromosome number of this species was also found to be 2n = 28 by Giusti, the same year (1989), in Argentina.

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G. R.
DÉPARTEMENT DES SCIENCES FORESTIÈRES
FACULTÉ DE FORESTERIE ET DE GÉOMATIQUE
UNIVERSITÉ LAVAL, SAINTE-FOY
QUÉBEC, CANADA G1K 7P4

C. G.
LABORATOIRE DE CYTOLOGIE ENVIRONNEMENTALE ET
DES RESSOURCES PHYTOGÉNÉTIQUES DU MENVIQ
DÉPARTEMENT DES SCIENCES FORESTIÈRES
FACULTÉ DE FORESTERIE ET DE GÉOMATIQUE
UNIVERSITÉ LAVAL, SAINTE-FOY
QUÉBEC, CANADA G1K 7P4

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EVOLUTION OF A FLORA: EARLY CONNECTICUT VALLEY BOTANISTS

C. JOHN BURK

ABSTRACT

The first known botanical studies of the Connecticut Valley in western Massachusetts were initiated during the decade 1810–19. Four area physicians, David Hunt of Northampton (1773–1837), Jacob Porter of Plainfield (1783–1846), Dennis Cooley of Deerfield (1789–1860), and Stephen West Williams of Deerfield (1790–1855), kept extensive personal herbaria and corresponded with Amos Eaton at Williams College and Benjamin Silliman at Yale. Porter, Cooley, and Williams published phenological accounts of local vegetation and other scientific observations. Beginning around 1816, Edward Hitchcock (1793–1864) commenced botanical studies at Deerfield that culminated in the first flora of the region, published at Amherst in 1829. Hitchcock acknowledged Cooley and Williams as "early coadjutors in this work," which served as a basis for Hitchcock's 1833 compilation of the Massachusetts flora.

Key Words: botanical history, Connecticut Valley, Massachusetts, David Hunt, Jacob Porter, Dennis Cooley, Stephen West Williams, Edward Hitchcock, Massachusetts flora

INTRODUCTION

The early 19th Century in both Europe and North America is "remarkable for the simultaneous appearance of groups of highly intelligent leaders with such broad interests from politics to philosophy and science that their impact on the future outweighed their numbers" (Billings, 1985). Nonetheless, sources of information on the development of botany in the Connecticut Valley in western Massachusetts throughout this period are scattered, fragmentary, occasionally contradictory, and often accessible only from archival sources and special collections. The purpose of this study is to assemble and synthesize information on botanical activities in the region from the earliest known studies through the completion of its first complete flora, Edward Hitchcock's "Catalogue of Plants Growing Without Cultivation in the Vicinity of Amherst College" (Hitchcock, 1829), a list which served as a major source for the first compilation of the Massachusetts flora (Hitchcock, 1833).

Hitchcock, by then a prominent geologist who had served as president of Amherst College, observed in his reminiscences

(Hitchcock, 1863) that Amos Eaton, who had lectured in Amherst and Northampton, Massachusetts in 1816 and 1817, was "the chief agent of introducing a taste for [natural history] into the Connecticut Valley" and that at the time "Dr. Stephen Williams, Dr. Dennis Cooley, and myself, all of Deerfield, took hold of mineralogy and botany with great zeal." Widely regarded as a charismatic teacher (Ballard, 1897), Eaton had in 1817 just recently published the first edition of A Manual of Botany for the Northern States (Eaton, 1817). This work described and classified all genera known to occur north of Virginia according to a modified version of the Linnean system and included brief descriptions of the more common species with notes on their occurrence in the vicinity of Williams College and elsewhere.

Despite Hitchcock's recollections, botanical work had been in progress in the Connecticut Valley for some years prior to the time of Eaton's lectures, and when Eaton published a much expanded and enlarged second edition of his manual in 1818, he was able to include within its catalogue localities for at least 91 species, indicated by the letter "N.," that occurred along the Connecticut River between Northampton and Deerfield. These were attributed to "Dr. D. Hunt, and Drs. Williams and Cooly (*sic*) of Deerfield" (Eaton, 1818).

The work of Eaton, which was largely done outside the area, and the geological contributions of Edward Hitchcock have been studied in some detail (Ballard, 1897; Foose and Lancaster, 1981; Knowlton, 1897; Smallwood, 1941). In addition, Jenny (1980, 1987) has recently described the "rediscovery" of the herbarium of Stephen Williams and the "small but highly competent group of botanists" who lived in Deerfield around 1816. However, the various and inter-related botanical contributions of Hunt, Williams, and Cooley, as well as those of Jacob Porter, whose plant lists from the area were later acknowledged both by Eaton (1822, 1824) and by Torrey and Gray (1838–40), are less well known, as is Hitchcock's early work in botany. In this paper, Hunt, Porter, Cooley, Williams, and Hitchcock are discussed chronologically according to their dates of birth. This chronological order is roughly correlated with the increasing importance of their contributions to the development of botanical science in the region and with the greater amount of information available on the later individuals.

DAVID HUNT

Information regarding the botanical activities of David Hunt (1773–1837) is particularly scarce. Hunt was a member of a well-established Northampton family and sufficiently prominent as a physician to be included by Stephen Williams in the American Medical Biography (Williams, 1845). Hunt was also described, in a tribute written long after his death, as "a botanist and mineralogist of considerable note" (Springfield Union, 1904). Williams, who knew Hunt personally, reported that Hunt maintained a correspondence with Benjamin Silliman and other academic scientists, belonged to several medical and scientific societies, and possessed a "cabinet of minerals" that was "rare . . . and large, for a private individual" (Williams, 1845). The Centennial Hampshire Gazette (1886) reprinted William's tribute, including a portrait of Hunt (Figure 1), along with additional biographical materials by Hunt's son Seth, who recalled that his father possessed a "large herbarium . . . very neatly and scientifically arranged and labelled, by his own hands" (Centennial Hampshire Gazette, 1886). Both David Hunt and his father Ebenezer Hunt were among the sponsors of Eaton's 1817 course of lectures in Northampton and signed a letter of commendation, included in the introduction of Eaton (1818), expressing their "entire satisfaction" with Eaton's work there. Although Porter (1821) reported at least one of Hunt's observations, that "Doctor David Hunt . . . has found at Northampton, numerous specimens of the sarracenia with yellow blossoms," Hunt apparently published nothing related to botany under his own name. Williams (1845) recalled only a single paper by Hunt in a medical journal, a paper on a case of lead poisoning, and concluded that "the productions of his pen were not numerous."

Hunt was married for nearly 42 years to Wealthy Dickinson, a descendent of one of the first settlers of Hadley, Massachusetts. The couple had thirteen children, ten of whom reached adulthood (Centennial Hampshire Gazette, Sept. 6, 1886.) In the first of his major geological papers, Edward Hitchcock acknowledged his "particular obligations" to Hunt and to Benjamin Silliman (Hitchcock, 1818), and Hunt's nonprofessional interests almost surely were centered more in geology than botany.

The location of Hunt's herbarium, if it still exists, is at present

Dr. David Hunt.

Figure 1. Dr. David Hunt, reprinted from Williams (1845) in Centennial Hampshire Gazette (1886). Courtesy of Historic Northampton.

unknown. Although the Amherst College "cabinet" during Hunt's lifetime included the only institutional herbarium in the area. Hitchcock (1863) does not mention Hunt's specimens among the botanical materials in the collections and I have not been able to identify any Hunt specimens in the Amherst College materials incorporated in MASS in the 1950's.

JACOB PORTER

Jacob Porter (1783–1846) was born in Abington, Massachusetts. He attended Williams College, but in 1802 transferred to Yale University, receiving an A.B. degree there in 1803 (Dexter, 1885–1912). He then moved to Plainfield, Massachusetts where he practiced medicine for the remainder of his life. He assembled a collection of plants and minerals from the vicinity (Porter, 1834) and, according to a local historian (Dyer, 1891), "although a highly educated man, gave his attention mostly to literary pursuits, being well versed in botany and mineralogy." In addition to poetry, translations of religious tracts, and a history and geology of Plainfield (Porter, 1834), Porter published two accounts of phenological phenomena (Porter, 1818, 1821). These were among a number of "floral calendars" published with the encouragement of Benjamin Silliman (Silliman, 1818) in the early volumes of The American Journal of Science. Silliman included these accounts in response to a memoir by Jacob Bigelow setting out research into "the comparative forwardness of the spring season in different parts of the United States" (Bigelow, 1818).

Plainfield is situated at an elevation of 1684 feet on the western edge of the Connecticut Valley watershed (U.S.G.S. topographic map, Plainfield Quadrangle, Franklin Co., Massachusetts), and Porter's first calendar, was intended to "show that vegetation is considerably later on the range of mountains, on which this place is situated, than in the level parts of our country." The paper was possibly also inspired by the well-publicized observations of Humboldt and Bonpland relating altitude to climate (Humboldt and Bonpland, 1805; Billings, 1985). Though neither author mentioned the other, Porter's data could be compared with similar though more extensive observations from Deerfield, Massachusetts in the Connecticut Valley to the east reported by Stephen Williams (1819) in the subsequent issue of The American Journal of Science. Williams, for example, found *Hepatica triloba* (*H.*

americana) and *Erythronium* (*E. americanum*) in flower on April 26, 1818 in Deerfield, Massachusetts at an elevation of 140 feet (U.S.G.S. topographic map, Greenfield Quadrangle, Franklin Co, Massachusetts), while Porter reported these taxa first blooming on May 1 of that year at the higher elevation.

Porter's second and more extensive calendar covers the 1819 season and 1820 through July 30 and includes the observations on *Sarracenia* by David Hunt with notes from a trip to Northampton. The work was abbreviated by Silliman in response to "objections to highly detailed floral calendars" (editorial comment in Porter, 1821); nonetheless, the entries for 1819 alone include observations of more than 280 taxa of higher plants. These are predominantly native species along with a number of crop plants and ornamentals. For most taxa, common names are carefully assigned and often include part of a Latin binomial; the entry for May 24, 1820, for example, includes "Caulophyllum, glaucous kalmia, painted trillium and water cress" in bloom. Porter's style is occasionally "literary" ("the petals of the roundleaved violet, in particular, resemble specks of gold scattered around the path" on May 6, 1819 in one instance), and he sometimes suggests herbal remedies, including a tincture of goldenrod root in brandy as a proven cure for spitting blood. In addition to its phenological information, the value of the work lies in its listing of a wide range of species from a diversity of natural habitats and from locations, such as the banks of the Westfield River and a bog in the town of Hawley, which are still botanically important.

Porter knew and corresponded with several academic scientists of the period; these include Hitchcock, who cites several species on Porter's authority (Hitchcock, 1829), Eaton, who, in the third (1822) and later editions of his Manual mentions Porter's "improvements in the localities of plants . . ." from "the mountain range in Plainfield, Hawley, and Cummington, Mass." and John Torrey and Asa Gray, who include him in a list of contributors of plants from Massachusetts (Torrey and Gray, 1838–40). He was a member of several scientific societies, including the Lyceum of Natural History of New York and the Massachusetts Society for Promoting Agriculture. His first wife, Betsey Mayhew, of Williamsburg, Massachusetts, died a few months after their marriage in 1813; his second wife, Sally Reed, outlived him for many years (Dexter, 1885–1912).

DENNIS COOLEY

Two short biographical sketches of Dennis Cooley (1789–1860) were published in the decades following his death. The first and longer of these (Kenaston, 1863) consists of a two page account of Cooley's life in connection with a set of resolutions accepting Cooley's herbarium, which his widow had donated to the Michigan State Agricultural College (now Michigan State University, East Lansing). This account is consistent with genealogical data in Sheldon (1895–96). The second, a two paragraph "sketch" by Beal (1901) is inaccurate in some details, including the year of Cooley's birth.

Dennis Cooley was born in the Bloody Brook section of Deerfield, Massachusetts in 1789 (Sheldon, 1895–96). The Cooley family had been prominent in that area for many years and like Hunt, Porter, and Williams, Cooley was educated as a physician. By 1816, he was studying medicine in the office of William Stoddard Williams and his son Stephen West Williams (Williams, 1849). He received a degree from the Berkshire Medical Institution in 1822 (Beal, 1901), and reportedly, ". . . his leisure hours, during his whole course of study, were spent in pastures, woods and swamps in pursuit of botanical specimens" (Kenaston, 1863). These botanical activities led to the 1818 contributions to Eaton and a "floral calendar" for Deerfield (Cooley, 1820) which, though brief, included a chart comparing seven phenological phenomena over a five year interval, beginning in 1815.

Correspondence (now in the Amherst College Archives) between Hitchcock and Silliman and between Hitchcock and John Torrey indicates that by the early 1820's, Cooley and Hitchcock had jointly prepared a manuscript catalogue of the Deerfield flora. The fate of the Cooley/Hitchcock manuscript is considered later in this paper. However, in a letter to John Torrey (Edward Hitchcock to John Torrey, Nov. 25, 1819 in President Edward Hitchcock Papers, Box 6, Folder 12, Amherst College Archives) Hitchcock commented that Cooley was not appreciated by the people of Deerfield, who felt that he neglected his medical practice for his botany; and subsequently, Cooley moved to Monticello, Georgia "to seek his fortune" according to Hitchcock, who urged Silliman to provide him with introductions, if possible, to southern botanists (Edward Hitchcock to Benjamin Silliman, Oct. 17, 1822,

Box 6, Folder 4, President Edward Hitchcock Papers, Amherst College Archives).

In Georgia, Cooley practiced medicine for about three years, a period "turned to a good account in his rapidly growing Herbarium" (Kenaston, 1863). For reasons of health, he returned North and eventually relocated to Washington Township, Macomb County, Michigan in 1827, taking his plant collections with him then or at a later date. Cooley's Massachusetts specimens alone represented, according to Hitchcock (1829), "nearly all the plants hitherto found in this district." In Michigan, Cooley began a study of the flora of Macomb County, sending lists of plants from that area to Eaton as early as 1829 (Eaton, 1829, 1833, 1836; Eaton and Wright, 1840). He was married to Elizabeth Anderson of Deerfield in 1830; the couple had two children, both of whom died in early childhood. Elizabeth Anderson died in 1834, and in 1836, Cooley married Clarissa A. Andrews, who survived him (Kenaston, 1863; Sheldon, 1895–96). Cooley apparently spent most of his later years in Michigan; the Memorial Libraries at Deerfield possess a single letter in his hand (Dennis Cooley to Eli Cooley, June 2, 1850, Cooley Family Papers, Pocumtuck Valley Memorial Association Library, Deerfield, Massachusetts) in which he says that he had thought of visiting Deerfield, "but i suppose that folks are not enlitened there and shall not come this year." Cooley continued the practice of medicine until 1856 and served as postmaster of Washington township until 1859 (Beal, 1901). In his reminiscences, Hitchcock (1863) reflected that Cooley "became an excellent botanist, and even at a recent date, when he died in Michigan, has pursued the subject with zest." His herbarium when presented to the Agricultural College was estimated to contain more than 20,000 specimens and described as "especially rich in our indigenous flora" with "a large collection of tropical, Californian, and Australian species . . . Many of the plants were obtained by exchanges with Dr. Torrey, W. S. Sullivant, Dr. Dewey, John Carey, and many other celebrated Botanists, . . ." (Kenaston, 1863). Beal (1901) stated the herbarium contained around 4000 specimens, and Jenny (1987) noted that the contradiction in these estimates had not been resolved. Possibly Beal may not have included the specimens obtained by exchange in his estimate.

The Beal-Darlington herbarium at Michigan State University now contains the Cooley collection, including material from Deer-

field collected between 1817 and 1821 (Jenny, 1987; Martha Case, pers. corresp.).

STEPHEN WEST WILLIAMS

Stephen West Williams (1790–1855) was also a physician and a member of a prominent Deerfield family. He attended Deerfield Academy and then studied medicine as an apprentice to his father, William Stoddard Williams, spending one winter as a student at Columbia College in New York (Huntington, 1881; Viets, 1936). By 1816, he was "enamoured" with the field of botany, inspired by readings in the works of Barton, Bartram, Bigelow, Cutler, Eaton, Elliott, Muhlenberg, Pursh, and others (Williams, 1849). He recorded botanical observations as early as 1811 (Williams, 1819); and, along with Cooley and Hitchcock, began collecting plants about 1816. By 1817 he had compiled an herbarium that included around 500 pressed specimens (Jenny, 1980, 1987).

This 1817 herbarium was privately held until recently when its botanical interest was recognized by Roberta Poland and its identity established by William Jenny (Jenny, 1980, 1987). The herbarium is now preserved at the Pocumtuck Valley Memorial Association Library at Deerfield, Massachusetts. It contains specimens of at least 360 taxa, ranging from common garden flowers to local rarities such as *Asplenium ruta-muraria.* These are mounted, often several to a sheet, in a bound volume, and vary from whole pressed plants to small portions of a single shoot or even single flowers. The specimens are identified by Latin and/or common names either written directly on the sheet or on a slip of paper attached to the specimen. Collection data, including localities and dates, are generally lacking.

In 1818, Williams married Harriet Goodhue of Deerfield, the daughter of Joseph Goodhue, an army surgeon (Viets, 1936). About this time, Williams prepared a companion volume to his herbarium, a handwritten manuscript now owned by the Flynt Library at Historic Deerfield (Jenny, 1987). It contains indices to the common and scientific names of the specimens in the herbarium, an outline of the Linnean system, and a description of each plant listed, its medicinal properties and other characteristics. Cultural directions for garden plants such as hyacinth and lilac are given, as are materials from various authors, including

a passage from Bartram describing *Sarracenia.* Harriet Goodhue drew and painted "from nature, and from other sources" a number of original illustrations for this interesting compilation, which also includes illustrations clipped from contemporary publications such as The Monthly Flora.

Also around 1818, Williams sent Benjamin Silliman a box of specimens of minerals to be identified, and, in responding, Silliman encouraged both Hitchcock and Williams to contribute to The American Journal of Science (Benjamin Silliman to Edward Hitchcock, March 1, 1818, President Edward Hitchcock Papers, Box 6, Folder 5, Amherst College Archives). In 1819, Williams published his accounts of phenological phenomena for the years 1811, 1812, and 1818. This more original work (Williams, 1819) seemingly has been confused by Viets (1936) with the manuscript companion volume to the herbarium in the Flynt Library, which was prepared at roughly the same period. The contrast between Williams's observations in the period 1811–12 and his observations in 1818 is striking and reflects his increasing taxonomic skills and interests. In 1811, he reported a number of phenological phenomena, particularly observations upon "the time of the germination, foliation, florification and frutification" of around 60 plant taxa, providing common names for all of these and scientific names for approximately half. Of the taxa listed, over two thirds were in cultivation as either ornamentals or crop or garden plants, while the remainder were natives such as bloodroot, *Sanguinaria canadensis,* or non-native ruderals, such as the dandelion (as *Leontodon taraxacum*). In 1812, he repeated observations on many of these and included information on an additional 14 taxa. In 1818, however, in addition to continued observations on the plants previously noted, he provided data on an additional 92 species, listing all of these by Latin binomials, with common names for most. The greater number of the 92 new entries are native species taken from a diversity of natural habitats, including wetlands (for instance skunk cabbage, as *Pothos foetida*) or upland woods (*Epigaea repens, Trillium cernuum*).

Although, his career centered on teaching medical jurisprudence, chiefly at the Berkshire Medical Institution with stints at Willoughby University in Ohio and the Dartmouth Medical School (Viets, 1936), Williams retained a lively interest in botany for the remainder of his life. He, along with Cooley, was acknowledged by Hitchcock as "among my early coadjutors" in the 1829 Cat-

alogue, and he reciprocally (Williams, 1849) recognized the importance of Cooley and Hitchcock and the early "botanical investigations" of Orra White, later Mrs. Hitchcock, to the development of botany in Massachusetts. He remained in communication with Amos Eaton and prepared etymologies for generic and subgeneric names that appeared in the 6th and later editions of the Eaton Manual. Throughout his career, he wrote extensively on the subject of medicinal plants (Deane, 1855); among the most important of these works was the catalogue of 319 indigenous medicinal plants of Massachusetts in Williams (1849).

As Professor of Medical Jurisprudence at the Berkshire Medical School at Pittsfield, Massachusetts, he became known as the leading medical historian and biographer of his day. He and Harriet Goodhue had four children, two daughters, both of whom prepared illustrations of medicinal plants for their father's lectures, and two sons, one of whom died in infancy. The second son was trained as a physician in his father's office and later settled in Laona, Illinois. Stephen Williams himself retired in 1853 to Laona, where, according to his daughter (Huntington, 1881), he spent his remaining days in study and "riding over the beautiful prairie, looking for new specimens of flowers, animals or birds."

EDWARD HITCHCOCK

Edward Hitchcock (1793–1864), was born at Deerfield, Massachusetts, and attended Deerfield Academy. Because of weakened eyesight, he abandoned plans to attend Harvard University and took a position as principal of Deerfield Academy, a post he held from 1815–19. By his own account (Hitchcock, 1863), he began his studies in natural history about the time of Eaton's 1816 lecture in Amherst, collecting, with Dennis Cooley, "nearly all the plants, phenogamous and cryptogamous in the valley." In 1817, he also initiated his lifelong correspondence with Benjamin Silliman at Yale (Robinson, 1979).

In 1818, Hitchcock informed Silliman that he had collected over 800 plants in the vicinity and that 150 of these had been painted by "Miss White" (Edward Hitchcock to Benjamin Silliman, Sept. 28, 1818, President Edward Hitchcock Papers, Box 6, Folder 4, Amherst College Archives). Orra White (1796–1863)

was a native of Amherst, Massachusetts who was teaching botany, among other subjects, at Deerfield Academy and who had already achieved some degree of success as a botanical illustrator (Jenny, 1987; Worman, 1989). In 1818, Hitchcock also undertook a course of studies for the ministry.

In 1819, Hitchcock initiated a correspondence with John Torrey, requesting help with the identification of a specimen of *Potentilla* (Edward Hitchcock to John Torrey, July 20, 1819, President Edward Hitchcock Papers, Box 6, Folder 12, Amherst College Archives). The following year he and Dennis Cooley promised Torrey a list of plants "growing spontaneously in Deerfield" (Edward Hitchcock to John Torrey, April 28, 1820, President Edward Hitchcock Papers, Box 6, Folder 12, Amherst College Archives) which had been sent by the end of the summer (Edward Hitchcock to John Torrey, September 8, 1820, President Edward Hitchcock Papers, Box 6, Folder 12, Amherst College Archives).

Shortly before his ordination to the ministry, Hitchcock and Orra White were married and after ordination, the couple moved to Conway, Massachusetts where Hitchcock served as pastor from 1821–25 (Foose and Lancaster, 1981). Hitchcock continued to pursue scientific interests at Conway, preparing both geological and botanical papers for The American Journal of Science. In 1822, he expressed concern to Silliman that Thomas Nuttall, who was visiting the area, was "exploring the country minutely" and that "it would be a little mortifying if the facts that I have been collecting should appear in Philadelphia first" (Edward Hitchcock to Benjamin Silliman, September 22, 1822, President Edward Hitchcock Papers, Box 6, Folder 12, Amherst College Archives).

At this time, Hitchcock and Dennis Cooley were preparing the catalogue of Deerfield plants intended for the American Journal of Science (Edward Hitchcock to John Torrey, November 3, 1822, President Edward Hitchcock Papers, Box 6, Folder 12; Edward Hitchcock to Benjamin Silliman, October 17, 1822, President Edward Hitchcock Papers, Box 6, Folder 4, Amherst College Archives). Cooley then moved from Deerfield to Georgia, leaving the catalogue for Hitchcock to finish (Edward Hitchcock to Benjamin Silliman, October 17, 1822, President Edward Hitchcock Papers, Box 6, Folder 4, Amherst College Archives). Silliman delayed in publishing the manuscript, however, "lest objections be made that too much space was allowed to communications from a particular quarter" (Benjamin Silliman to Edward Hitch-

cock, December 5, 1822, President Edward Hitchcock Papers, Box 6, Folder 5, Amherst College Archives), and in 1823 returned the manuscript to Hitchcock, leaving "any further disposition of it to your better judgement" with the suggestion that the work should be revised as two papers with cryptogams treated separately (Benjamin Silliman to Edward Hitchcock, May 5, 1823, President Edward Hitchcock Papers, Box 6, Folder 5, Amherst College Archives). At least two manuscript volumes of Orra White Hitchcock's botanical work survive from this period, a collection of watercolors of grasses and other flowering plants entitled *Herbarium parvum, pictum* dated "1817,18" and now in the Archives of Deerfield Academy (Jenny, 1987; Worman, 1989) and a sketchbook of fungi entitled *Fungi, selecti picti,* dated 1821 and now in the Smith College Archives. Figure 2 reproduces a representative page from the latter manuscript; thirteen different fungi are depicted on the page; all but one is identified at least to genus. The individual fungi are numbered, but the numbers are not always consecutive, ranging on this page from 14 to 61; the numbers thus may refer to numbered specimens in a collection or included in a list.

Meanwhile, in a second major paper on the geology of the region, Hitchcock (1823a) included "occasional Botanical notices" that related a number of plant species to underlying rock types and landforms, including a series of cryptogams associated with mica slate. His discovery in a hilly pasture of *Botrychium simplex* (Hitchcock, 1823b) was the "first new fern described by an American" (Tryon, 1969), and he also published observations on *Gyropodium coccineum,* a new genus and species of fungus described by Schweinitz and first seen at Deerfield by Dennis Cooley (Hitchcock, 1825). Orra White Hitchcock continued her work in scientific illustration, including drawings to accompany her husband's publications and the drawings for Chester Dewey's publications on the genus *Carex.* Contrary to Fernald (1950), *Carex hitchcockiana* was named by Dewey (1826) in honor of both Edward and Orra White Hitchcock, the "lady, to whom I am so greatly indebted for the figures which accompany this Caricography."

In 1825, Hitchcock left the ministry, taking an appointment as the first Professor of Natural History and Chemistry at Amherst College. At Amherst, Hitchcock's interests turned increasingly to the field of geology, a subject that, throughout his life, he at-

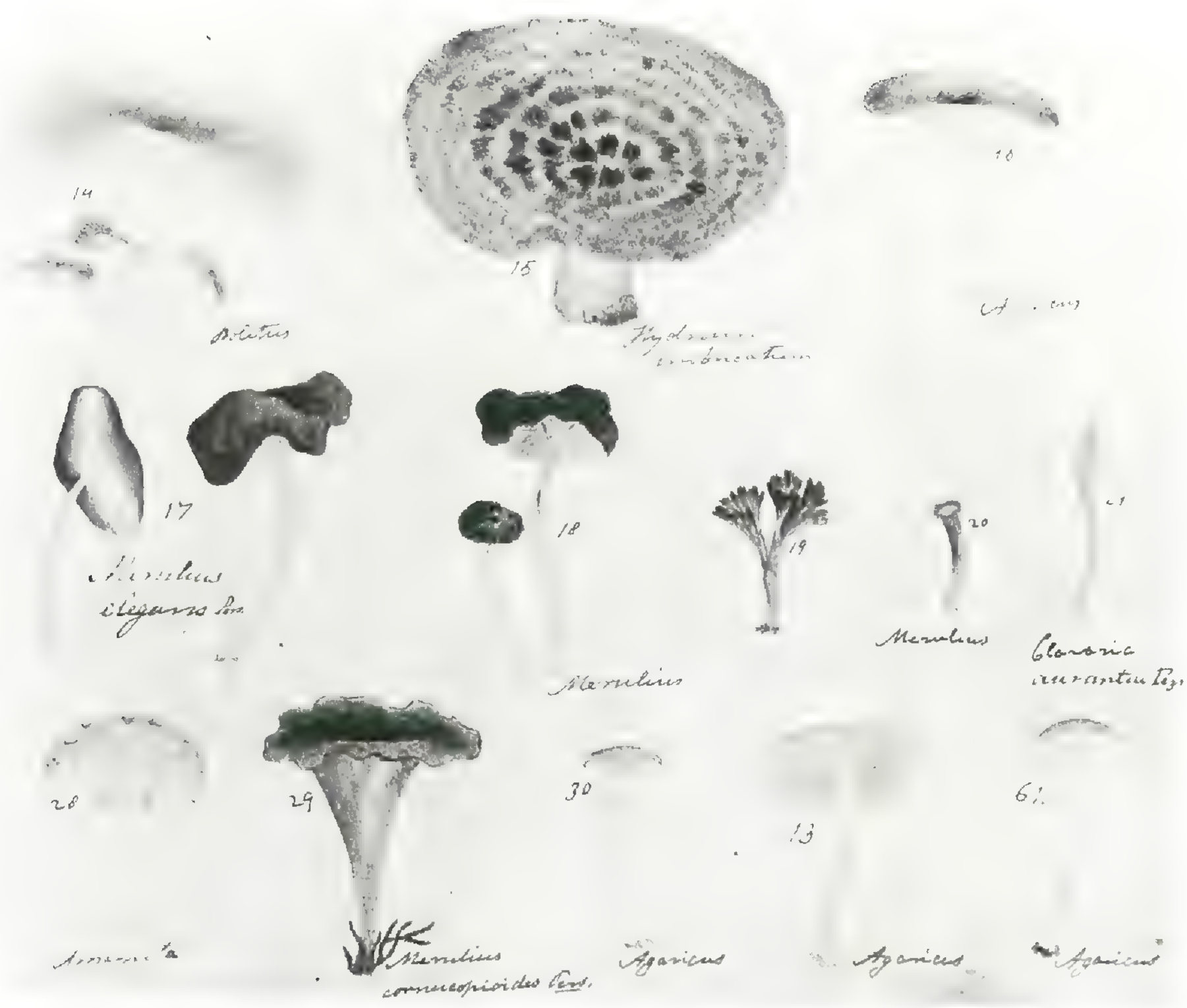


Figure 2. Representative page from Orra White Hitchcock's manuscript sketchbook *Fungi, selecti picti* (1821). Courtesy of Smith College Archives.

tempted to reconcile with the tenets of religion (Foose and Lancaster, 1981; Robinson, 1979). Nonetheless, he continued botanical studies and maintained a correspondence on his botanical discoveries in the Amherst area with Torrey. Among the latter were what he believed to be a new species of *Malaxis* (Edward Hitchcock to John Torrey, July 5, 1827, President Edward Hitchcock Papers, Box 6, Folder 12, Amherst College Archives) that he had found on Mt. Holyoke on a field trip with his botany class and which he hoped to publish as *Malaxis holyokea* "in the hope of exciting more zeal in natural history among the students here."

In 1829, at the request of the members of the Junior class who were attending his lectures in botany, Hitchcock published the Catalogue of Plants Growing Without Cultivation in the Vicinity of Amherst College. Apparently no copy of the Hitchcock-Cooley manuscript that Silliman declined to publish now exists; hence it is impossible to determine how that differed from the published

Hitchcock catalogue. The Hitchcock catalogue was intended to include "all the indigenous and naturalized plants, that have been discovered and ascertained, within forty or fifty miles of Amherst College" and, in addition, "such as are peculiar to the White Mountains and the sea coast of New England" plus "a few others mentioned on account of their being rare and interesting." Examples of the latter include the prickly pear, *Cactus opuntia* L. (now *Opuntia humifusa* Raf.) from "East Rock, New Haven."

Phenogamous plants, both angiosperms and gymnosperms, were listed alphabetically by genus, with species alphabetized within the genera. This resulted in such blatantly "unnatural" sequences as genera 197, 198, and 199 which are *Juncus, Juniperus,* and *Kalmia* respectively. Members of the class Cryptogamia were organized alphabetically by genera under orders Filices, Musci, Hepaticae, Algae, Lichenes, and Fungi with species alphabetized by genera under their respective genera. Excluding species from the White Mountains and the seacoast or included only because they were rare or interesting, the Catalogue included by Hitchcock's own count 1447 species within 531 genera that occurred within 50 miles of Amherst. Of these, 997 species in 395 genera were phenogamous while 450 species in 136 genera were cryptogams.

Localities were given for rare plants in the vicinity, including sites attributed to Dewey, Eaton, and Porter. Some of these, including Eaton's record of *Liquidambar styraciflua* from Northampton, Porter's *Orontium aquaticum* from Southwick, and an unattributed report of *Listera cordata* from Plainfield, remain of considerable interest.

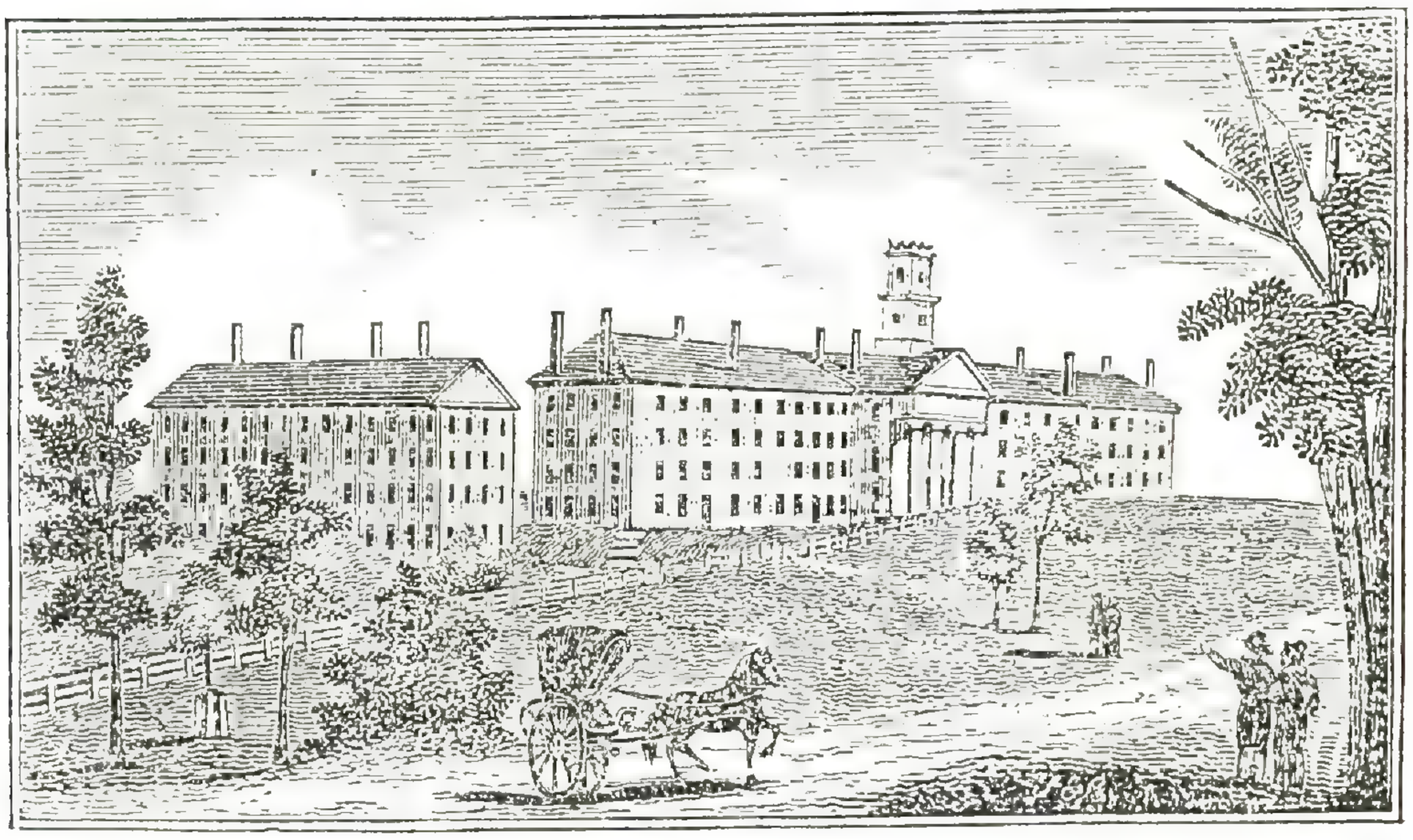
In 1830, Hitchcock was appointed to head a survey of the geology, mineralogy, botany, and zoology of Massachusetts (Foose and Lancaster, 1981). The initial report of the survey (Hitchcock, 1833) contained a catalogue of the flora of Massachusetts. This was organized according to a "Natural System of Prof. Lindley as adapted to North American Plants by Torrey" and based on Hitchcock's 1829 Catalogue with additions and corrections along with lists published by Dewey (1829) and by Bigelow (1824) and a manuscript flora of New Bedford and Nantucket by Thomas A. Green. W. S. Tyler, who knew Hitchcock both as a teacher and as a colleague, observed (Tyler, 1873) that Hitchcock "did but one great work at a time. But he was never afraid of having too many smaller irons in the fire." Nonetheless, the Massachu-

Figure 3. Edward Hitchcock, engraving in Tyler (1873). Courtesy of Forbes Library, Northampton, MA.

setts Catalogue was apparently Hitchcock's last botanical contribution. The report of the survey (Hitchcock, 1841) dealt only with the geology of Massachusetts, and in 1845, Hitchcock was appointed president of Amherst College, a position he occupied until 1854, when he returned to another decade of teaching, writing and research. The engraving included in Tyler's *History of Amherst College* (Figure 3) shows Hitchcock in his later years.

Hitchcock's plant collections, however, formed the "nucleus" of the Amherst College Herbarium (Goodale, 1932). This herbarium, if founded in 1829, the year of the publication of the Catalogue, was according to Ewan (1969) the second institutional herbarium established in the United States. [The first herbarium in the United States was apparently at the Academy of Natural Sciences in Philadelphia, an institution "destined to receive the nation's oldest plant collections" (Ewan, 1969).] Figure 4 is a view of Amherst College published in 1839 (Barber, 1839); the herbarium probably was located in the building with the tower. Day (1901) noted that the Amherst College herbarium contained "plants of local interest, many of which are no longer found growing in the vicinity," and Stone (1913) reinforced Day's statement in his assertion that "Some of the plants observed by Dr. Hitchcock nearly a century ago and included in this list have not been found since his time, and others have become rare." Archival materials related to the Amherst College Herbarium are virtually nonexistent at either Amherst College or at the University of Massachusetts, where the collections were incorporated in MASS in the 1950's. Those Hitchcock specimens I have seen have almost certainly been remounted at some time. They consist of a pressed plant or part of a plant taped to an herbarium sheet with a small handwritten label on discolored stock usually pasted in the lower left corner. The label contains the name of the plant and often a date and/or location; the labels seem to be in Hitchcock's hand, as seen in his correspondence at Amherst College. In at least one instance, the handwritten label is mounted attached to the specimen itself. The collector's name does not appear on the handwritten slip, but a printed label attached in the lower right contains the statement "ex Herb Edward Hitchcock, LLD."

There are, however, in MASS a group of specimens from the Amherst College herbarium that have been remounted in a manner similar to those from the Hitchcock collection with older



North-western view of Amherst College.

Figure 4. "North-western view of Amherst College," engraving in Barber (1839).

discolored handwritten labels pasted on the left and printed labels on the right. As in the Hitchcock specimens, the handwritten label does not identify the collector, but unlike the Hitchcock specimens, the printed label also bears no reference to collector. These anonymous collections may well represent the "few hundred species of plants in the vicinity . . . previously prepared, I believe, by members of the College" in Hitchcock's 1863 account; if so, they would also represent early 19th century plant collections from the area.

Edward Hitchcock and Orra White had eight children, two of whom died in infancy. One of their daughters, Emily Hitchcock Terry (1838–1921), was a pioneer illustrator of the Minnesota flora and an early contributor to Rhodora (Smith, 1992).

Hitchcock's 1829 Catalogue was not reprinted or revised until after his death; it then underwent three expansions and revisions in less than 40 years (Tuckerman and Frost, 1875; Cobb, 1887; Stone, 1913). It remains an essential document for understanding both the flora and the development of botanical sciences in the Connecticut Valley region of western Massachusetts in the early 19th Century.

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DEPARTMENT OF BIOLOGICAL SCIENCES
SMITH COLLEGE
NORTHAMPTON, MA 01063

RHODORA, Vol. 96, No. 885, pp. 97–101, 1994

NEW ENGLAND NOTE

GLYCERIA MAXIMA (POACEAE) IN NEW ENGLAND

JEANNE E. ANDERSON AND A. A. REZNICEK

Tall Mannagrass, *Glyceria maxima* (Hartman) Holmburg is a stout perennial Eurasian grass found as a native species throughout most of northern Eurasia from the British Isles east to Japan and Kamchatka, albeit absent from the extreme north and most of the southwest of this range. (Tutin et al., 1980; Freckmann and Reed, 1979). Dore and McNeill (1980) provide one of the few keys among North American manuals which distinguishes *G. maxima* from the relatively similar *G. grandis*. They separate *G. maxima* by the length of the lower glume (2–3 mm versus 1.2–1.5 mm in *G. grandis*) and by the ascending and stiff panicle branches and rough sheaths versus nodding panicle branches and smooth sheaths in *G. grandis*. Fernald (1950) also distinguishes *G. maxima*, but under the name *G. spectabilis* Mert. & Koch. The synonymy ascribed to *G. maxima* is thoroughly detailed by Freckmann and Reed (1979).

Glyceria maxima was collected in the United States for the first time in 1975 in Racine County, Wisconsin (*Wilhelm & Schulenberg 2161* MOR). A second collection located approximately 12 miles east of the first collection in Oak Creek, Milwaukee County, WI was made in 1979. (*Reed s.n.* UWSP). Both collections were reported in 1979 publications (Swink and Wilhelm, 1979; Freckmann and Reed, 1979).

Glyceria maxima has been twice reported erroneously from the United States, Jordal (1951) reported *G. maxima* from near Fairbanks, Alaska, but the specimen (*Jordal 3539*, MICH) is *G. grandis*. More recently, an historical record of this species (as *Glyceria maxima* subsp. *maxima*) from Mattituck, Long Island (*Latham 35967*, NYS) mapped in the Preliminary Vouchered Atlas of New York State Flora (New York Flora Association, 1990) has proven to be a large individual of *G. canadensis* (Gordon Tucker, pers. comm., 1992).

Three populations of *Glyceria maxima* were discovered and mapped by Marc Lapin in 1990 on the Massachusetts Audubon Society's Ipswich River Wildlife Sanctuary in the towns of Topsfield and Wenham, Essex County, Massachusetts (Lapin, 1990).

A fourth population, also in Wenham, was located by Tim Smith in 1993. Voucher specimens were identified by A. A. Reznicek as cited below. Specimens examined: Massachusetts. Essex County: Wenham, Ipswich River Wildlife Sanctuary, Great Wenham Swamp (behind Perkins Island), 23 Jul 1992, *Anderson s.n.* (MICH); Topsfield, Ipswich River Wildlife Sanctuary, Mile Brook Swamp, 6 Aug 1992, *Anderson s.n.* (MICH). An additional voucher from the Wenham site has also been deposited: *Anderson s.n.* October 9, 1992 (NEBC). These collections are the first for New England and represent the third documented occurrence in the United States.

The Wenham population, within a high marsh system of the Great Wenham Swamp, forms a near monoculture of about two-thirds of an acre. There is a dense, but relatively shallow rhizome system reaching about half a meter in depth. Aerial shoots exceed two meters in height. Only a few individuals of *Cephalanthus occidentalis, Fraxinus pennsylvanica,* and *Lythrum salicaria* persist within this patch. The grass is also growing in a smaller stand, 6.5 meters square, located roughly 60 meters southeast of the larger Wenham population close to an edge of Perkins Island.

The Topsfield populations both occur within a shrub swamp community along Mile Brook, a tributary of the Ipswich River. The largest of these patches covers 2 acres. A portion of this population exists as a floating mat of individual plants and rhizomes which can be readily dislodged if disturbed. Downstream along the stream channel, a smaller stand measures about 15 meters in diameter. Sampling completed in one section of this swamp in 1990 determined that four non-native species, *Glyceria maxima* (sub *G. septentrionalis*), *Rhamnus frangula, Iris pseudacorus,* and *Lythrum salicaria* accounted for 67% of the relative cover within this community. Of these, *G. maxima* was the most prevalent species providing 39% of the relative cover (Anderson, 1991). This larger patch is discernible at least as far back as 1957 on black and white aerial photographs, however, *G. maxima* was not reported for Essex County by Harris (1975).

Dore and McNeill (1980) and Dore (1947) note that the first herbarium specimens of this species in North America were collected from the vicinity of Hamilton, Ontario, Canada in 1943. They also report that the species' distribution in the New World is concentrated primarily in Ontario. Other stands are known from Somenos Lake, British Columbia (*Calder & MacKay 31984*

DAO) and St. Johns and Brigus, Newfoundland (Day, 1991; Rouleau and Lamoureux, 1992). The specimen reported in Scoggan (1978) from northern Alberta has been determined to be *G. grandis* (Susan Aiken, pers. comm., 1992).

Glyceria maxima is a large, aggressive species with the ability to form huge stands in wetlands. Freckmann and Reed (1979) noted that *G. maxima* dominated at least 15 acres of the Oak Creek site in 1979. This invasive tendency has been evident in Ontario over the past fifty years and has been a subject of study in Europe (e.g., Buttery and Lambert, 1964). Even within its native range, the ability of *G. maxima* to create virtual monocultures under varying levels of disturbance is of conservation concern. Burgess et al. (1990) report that the swamp community type dominated by *G. maxima* more than doubled its area in the Ouse Washes, England between 1972 and 1988, largely in response to an overall increase in the incidence of summer flooding. This spread of *G. maxima* has reduced plant species diversity on the site, and as a consequence, reduced the number of seed-producing plants (particularly within the Cyperaceae and Polygonaceae) available to wintering seed-feeding ducks. *G. maxima* is reported to be a poor foodplant for wintering grazing waterfowl and a poor nesting substrate for many common wetland species (Burgess et al., 1990).

The spread of *Glyceria maxima* in the United States should be carefully monitored as it has the potential to be a very serious invader of natural wetlands. Vegetative dispersal is reported from Canada, where 53 separate stands of *G. maxima* were located in one thirteen mile stretch of the Mississippi River in Ontario (Gutteridge, 1954). The reliance on vegetative mechanisms of reproduction and dispersal is also suggested by Dore's (1953) report that only 1 to 9% of the florets set good grains. Further information on the spread of existing North American populations, coupled with additional data on dispersal mechanisms and control methodologies should be gathered before the species becomes thoroughly entrenched.

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We are grateful to Gordon Tucker and Susan Aiken for checking the identity of the specimens supporting the New York and Alberta reports of *Glyceria maxima* respectively. Jacques Cayouette

kindly sent us a great deal of information about the Canadian distribution of this species. Bob Freckmann and Ted Cochrane similarly sent us useful information on the Wisconsin sites. Pamela B. Weatherbee alerted us to the literature on one of the Wisconsin populations of *G. maxima,* for which we are thankful. Thanks are also extended to Les Mehrhoff, Sally Rooney, Mark Anderson, Michael Taylor, Roberta Lombardi, Jody Hall, and Keith Killingbeck for review of vouchers at their respective herbaria.

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J. E. A.
MASSACHUSETTS AUDUBON SOCIETY
SOUTH GREAT ROAD
LINCOLN, MASSACHUSETTS

A. A. R.
THE UNIVERSITY OF MICHIGAN HERBARIUM
NORTH UNIVERSITY BUILDING
ANN ARBOR, MICHIGAN 48109-1057

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NEW ENGLAND NOTE

NOTES ON THE RHODE ISLAND FLORA

Richard L. Champlin

The following list includes plant species found and collected by the author over a period of years, proving that even in the smallest state one can turn up species new to the area or otherwise of interest botanically. Specimens of all species have been sent to the Herbarium of the New England Botanical Club.

Thelypteris palustris (Salisb.) Schott var. *pubescens* (Laws.) Fern.

A far cry from their usual habitat, specimens of the Marsh Fern grow in Newport, RI. not in an open, sunny marsh, but next to the mortar cementing together the granite stonewall of a private estate. About three feet above the sidewalk they share the extraordinary habitat with *Woodsia obtusa* and *Asplenium platyneuron.* In five years of observation I have failed to find these Marsh Ferns fruiting, but the sterile fronds have all the diagnostic traits of the species—forking veins, the frequent twist of the whole frond, smooth green axis, black rootstock, etc.

Dryopteris filix-mas (L.) Schott

When Frederick Law Olmsted (1822–1903) designed the landscape in Newport for John W. Auchincloss in 1887 at the estate known as Hammersmith Farm, he included a rock garden for alpine plants. It consisted of a long trench blasted out of calcium-bearing shale. A bed of the Dryopteris was planted along the north ridge. Not only has the fern survived, it has flourished, and its spores have developed new plants in various parts of Newport, three of which have been located so far. Male fern, a mountain dweller, has come down to altitudes of less than one hundred feet.

Panicum amarum Ell.

M. L. Fernald's 8th Edition of Gray's *Manual of Botany,* 1950, puts Connecticut as the northernmost range of this grass. But it has reached Rhode Island and was found along Narragansett Bay at Plum Point, Saunderstown (Washington County) in 1989. It grows on the beach with *Prunus maritima,* and occasional Geasters.

Carex kobomugi Ohwi

This exotic carex occurs on Rhode Island sand dunes at East Beach, Charlestown (Washington County), found and collected in 1981.

Epipactis helleborine (L.) Crantz

This orchid has found a congenial habitat along a busy street in the City of Newport. One of its several locations is under the spread of another European species, the European Hornbeam, *Carpinus betulus*.

Epifagus virginiana (L.) Bart.

An even more striking example of adaptability than the above is the case of the Beech Drops. This saprophyte grows in eastern North America under the American Beech (*Fagus grandifolia*). In Newport, however, it has become established under a specimen of European Beech (*Fagus sylvatica*) on an estate where many European Beeches have come to maturity, but no American Beeches. The nearest known occurrence of Beech Drops and American Beech is about twelve miles away. The *Epifagus* is not known to grow natively in Europe, which makes this choice of habitat all the more surprising.

Morus rubra L.

Rhode Island does not fall within the natural distribution range of the Red Mulberry. Yet in Foster (Providence County) on the outskirts of the Lester Steere apple orchard grow without cultivation five specimens of the fruit-bearing tree. The probable explanation? This land in the nineteenth century was a cherry orchard. In that age, amid their cherries, orchardists planted Red Mulberries, which ripen simultaneously with the cherries. Thus they hoped to draw the bird population away from the cherries to the less valuable fruit. These specimens have apparently escaped to the surrounding, rich woods where they grow in company with Christmas fern, Basswood, Butternuts, and white Baneberry.

PRISCILLA ROAD
JAMESTOWN, RHODE ISLAND 02835

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NEW ENGLAND NOTE

DESMONEMA WRANGELLII (AG.) BORNET ET FLAHAULT, A NEW RECORD FOR MAINE

L. C. Colt, Jr.

Key Words: *Desmonema, Scytonema,* freshwater, basalt

During a field trip in search of *Micropterus dolomieui* Lacepede in south-central Maine, my collecting gear got caught on the rough and irregular surface of a massive basalt rock partially submerged in the water of Crawford Pond, Union, Maine. This pond in Knox County has been previously described (Colt, 1977, 1985). This rock surface lies on the east side of the large central island in the northern section of the pond, and is identified by the presence of several bronze plaques attesting to the unfortunate but accidental deaths of several people in that area of the pond's waters.

While retrieving my collecting gear I found that the entire surface of the rock below the water line was covered by a brownish felt-like mat of microscopic plants. Several samples of the plants were gathered and preserved in Transeau's Fluid (Prescott, 1962) since the proper equipment for examination of the samples was not immediately available.

Subsequent examination of the plants with a light microscope in my laboratory at the University of Massachusetts Dartmouth revealed that the plants were a cyanophyte alga, and using Smith (1950), the plant was identified as *Desmonema wrangellii* (Ag.) Bornet et Flahault 1887. The characteristics of the Maine plants matched the description by Smith, and subsequently, the descriptive material in Tilden (1910). Smith notes that the plant has parallel trichomes within common sheaths, and penicillate tufts which readily dissemble upon removal from the substrate. Tilden adds that heterocysts are basal, the plant mass caespitose and penicillate, and the filaments somewhat dichotomously divided. The summary environmental characteristics provided by VanLandingham (1982) generally fit. Although my plants were collected in a pond, there is frequent wind-aided water drift in the vicinity of the rock surface, along with small wave action, thus moving water is present, a characteristic of *Desmonema* habitat reported to frequently occur.

Drouet, in his monumental Revision of the Nostocaceae with Cylindrical Trichomes (1973), placed *Desmonema* in synonymy with *Scytonema hofmannii* Ag. According to Drouet, the plant identified by Bornet & Flahault as *Desmonema* is the same as the plant named *Thorea* by Agardh in 1812, as *Oscillatoria* by Agardh in 1813, as *Calothrix* by Bornet et Flahault in 1887, as *Coleodesmium* by Borzi in 1887, and as *Dillwynella* by Kuntze in 1891.

Drouet (1973) reduced the Nostaceae with cylindrical trichomes to three genera by characterizing the morphology of the terminal cells in the following manner.

Scytonema:	Terminal vegetative cells at first hemispherical, becoming almost spherical
Calothrix:	Terminal vegetative cells at first hemispherical, becoming blunt-conical or cylindrical with rotund tips.
Raphidopsis:	Terminal vegetative cells at first hemispherical, becoming more or less acute-conical.

Not all cyanophyte specialists agree with Drouet's revision. While Drouet examined an enormous number of specimens, more than 30,000, in researching his revisions of the cyanophytes, he came to depend on such characters as granulation (among the Oscillatoriaceae) and the shape of the terminal cell of the vegetative portions of the plants in both the Oscillatoriaceae and the Nostocaceae. Drouet (1973) states that the constant features of morphological value in classification of the Oscillatoriaceae are those of the protoplast alone. The characteristics of the external sheath, according to Drouet, are the products of the history of the environment and as a result, prove to be of no value for the purposes of classification. He further notes, writing about the Oscillatoriaceae, that the "end of a fragmented trichome proceeds, under favorable environmental conditions, to assume a configuration characteristic of the species".

There seems to be no disagreement among cyanophycologists that there is a great deal of morphological variation among the blue-green algae, and that this variation is primarily a function of environmental or habitat variation. Baker and Bold (1970) in their two-year culture studies in the Oscillatoriaceae note that the vegetative terminal cells in their cultures showed considerably more morphological variation than Drouet's work would seem to allow as permissible. Kathleen Baker of the University of Ha-

waii (Pers. comm.), who was kind enough to respond to my query on *Desmonema,* suggested that much work remains yet to be done by microbiologists to fully establish the relationships among the cyanophytes.

While my plants show the hemispherical-approaching-spherical cells of *Scytonema,* my experiences with desmid (Desmidiaceae) cells, where morphological changes in the new vegetative semicells appear to be the result of environmental factors present immediately prior to or during their development, leads me to wonder if such dependence on the morphology of one cell is appropriate. New desmid semicells can and do show distinct morphological differences from the parent (semicell), and if these changes persist into the next vegetative generation, subsequent observations can lead to the erroneous conclusion that the "new" semicells represent a new taxon. I suggest that what are needed are discrete studies at the molecular level which would identify the relationships among or the differences between the many already described cyanophyte taxa. I am aware that some studies have been undertaken, but these few appear to represent only a minute fraction of what is needed to clearly and accurately define the cyanophytes.

When I checked the New England Algal Data Bank (NEADB, 1993) to determine whether or not this plant had been previously collected in the New England Region, the only reported collection was by W. A. Setchell (1895) in New Haven, Connecticut. Given the large number of plants at the Maine site, the lack of other collections in New England seemed curious. Geitler (1932) reports *Desmonema* as being collected in England and the Pyrenees, and Whitford and Schumacher (1969) and Cocke (1967) report *Desmonema* from North Carolina, but I am not aware of any other reports from New England.

Given Drouet's assignment of *Desmonema* to *Scytonema,* it seemed reasonable to determine whether or not *Scytonema hofmannii* had been reported in New England. According to data in the NEADB Conn and Webster report *S. hofmannii* in Middlesex, County, CT, in 1908, and Holden is reported in both Tilden (1910) and Hylander (1925, 1928) to have collected it in Litchfield County, CT. Setchell (1896) collected *S. hofmannii* in Norfolk County, Massachusetts, and Collins (1904b) collected *S. hofmannii* in Grafton County, New Hampshire. The latter two collections are noted in Tilden (1910). Bailey (1847b) reported *S.*

hofmannii from Providence County, Rhode Island, and Flint (1916) collected *S. hofmannii* in Chittenden County, Vermont. The question is, do these all represent the same species, *Scytonema,* as reported by Drouet?

In that my own research is with certain of the chlorophytes, I feel somewhat uneasy in making any final determination on the systematic position of the cyanophyte plants which I collected in Maine. Despite the conclusions of Drouet, however accurate as they may eventually be shown to be, and given the uncertainties expressed in the literature and by personal communication I believe the appropriate action at this time is to report the collection of *Desmonema wrangellii* (Ag.) Bornet et Flahault for the second time in New England and for the first time in Maine.

I am indebted to Robert K. Edgar of the University of Massachusetts Dartmouth for access to his personal library and for his taking the time to assist in searching for clues to the systematics of this cyanophyte enigma.

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DEPARTMENT OF BIOLOGY
UNIVERSITY OF MASSACHUSETTS DARTMOUTH
N. DARTMOUTH, MA 02747

RHODORA, Vol. 96, No. 885, p. 109, 1994

THE BIOLOGY AND TAXONOMY OF THE *PORTULACA OLERACEA* L. COMPLEX IN NORTH AMERICA: ERRATUM

JAMES F. MATTHEWS

Figure 3, page 170, is incorrect. The seed surface shown is that of a stellate tuberculate *Portulaca pilosa* L. The seed surface pattern for the specimen labelled *Portulaca retusa* Engelm. as cited in Table 3, page 178, is shown here.

MATTHEWS, JAMES F., DONNA W. KETRON, AND SANDRA F. ZANE. 1993. The biology and taxonomy of the *Portulaca oleracea* L. complex in North America. Rhodora 95(882): 166–183.

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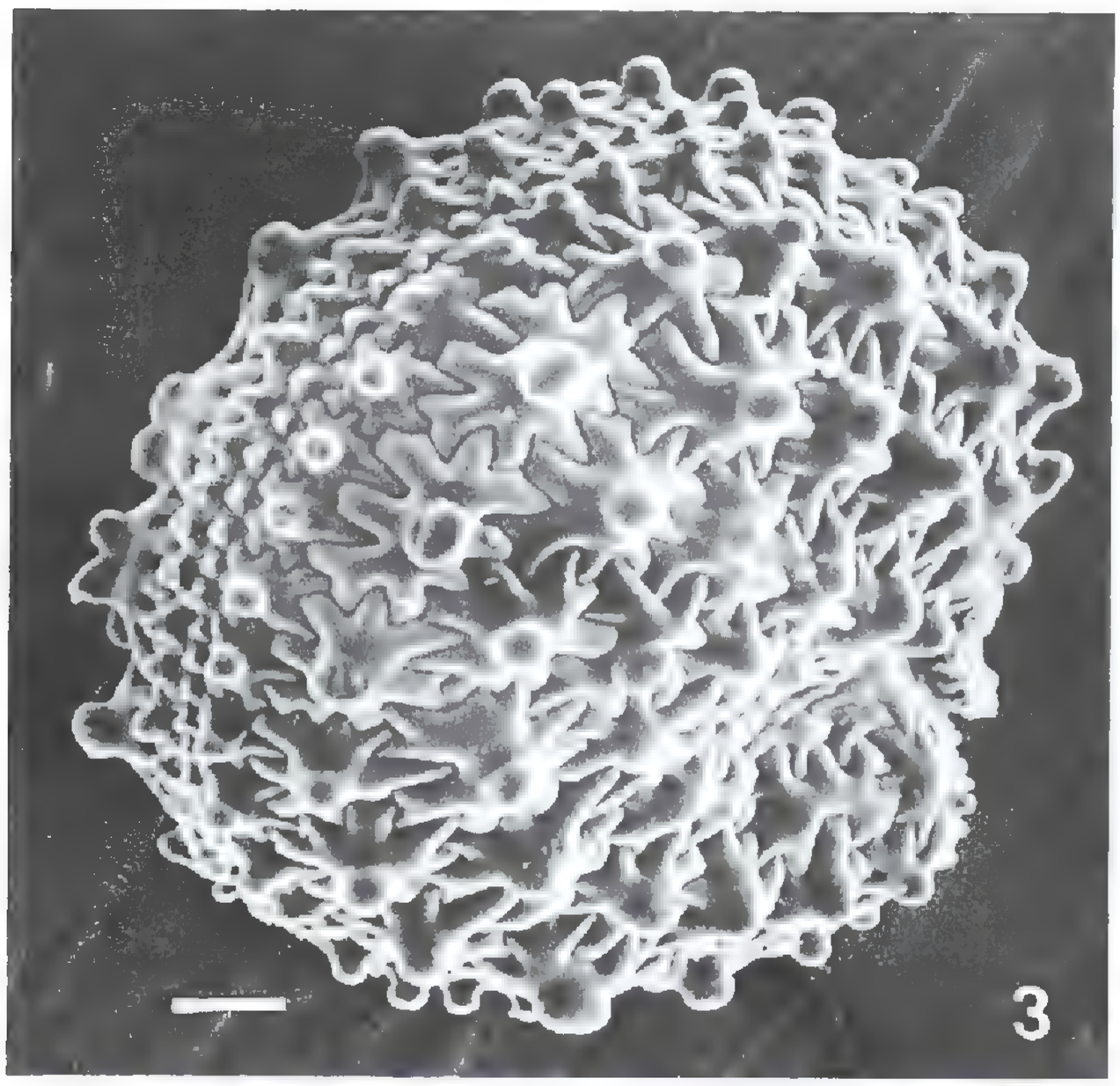

RHODORA, Vol. 96, No. 885, p. 110, 1994

BOOK REVIEW

Cheryl McJannet, George Argus, Sylvia Edlund, and Jacques Cayouette. 1993. *Rare Vascular Plants in the Canadian Arctic.* Syllogeus Series No. 72. Canadian Museum of Nature. Prepaid orders available from the Canadian Museum of Nature, Direct Mail Section, P.O. Box 3443, Station "D," Ottawa, Ontario, Canada K1P 6P4. (Price $17.95 U.S. and overseas, $14.92 Canadian orders).

This 79 page booklet covers the 236 rare vascular plant taxa found in the Canadian Arctic. A typical entry includes name, synonymy, family, phytogeography, where found in the Canadian Arctic, and its status in the various Provinces and the Northwest Territories. Each entry also contains a dot range map.

This is a valuable publication for those interested in the arctic flora. It follows the format for the other publications dealing with rare plants in the Canadian Provinces. The price seems excessive for such a publication. Mail orders must be prepaid by check, Visa, or Mastercard.

C. BARRE HELLQUIST
DEPARTMENT OF BIOLOGY
NORTH ADAMS STATE COLLEGE
NORTH ADAMS, MASSACHUSETTS 01247

RHODORA, Vol. 96, No. 885, pp. 111–112, 1994

BOOK REVIEW

Bernard Boivin. 1992. *Les Cypéracées de l'est du Canada.* Provancheria 25, Herbier Louis-Marie, Universite Laval (230 pp., including 69 figures). In French. Available from Herbier Louis-Marie, Faculté des sciences de l'agriculture et de l'alimentation, Université Laval, Quebec, Canada, G1K 7P4.

This treatment of the sedges of the six eastern provinces of Canada (Ontario, Quebec, New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland/Labrador) is the first segment of the *Flore de l'est du Canada,* planned as a series in Provancheria by Bernard Boivin, one of the outstanding botanists of this century. A student of both Marie-Victorin and Fernald, his work in floristics and taxonomy was wide-ranging and critical, and is best represented by the *Énumération des plantes du Canada* (1967), and in the 5-part Flora of the Prairie Provinces (1979). Written by Boivin before his death in 1985 at age 68, the Cyperaceae section was edited for publication by Paul Catling and Jacques Cayouette of Agriculture Canada, who are responsible for an up-to-date bibliography for the Cyperaceae in eastern Canada and a list of new records for this region discovered after Boivin's completion of the manuscript.

The flora includes two new taxa (one nothospecies, one new form) and ten new combinations. The twelve genera (*Hemicarpha* is included in *Scirpus*) and 217 species are represented, with an additional thirty nothospecies. *Carex* includes 168 species and 29 nothospecies. Each taxon is provided with a short description and a discussion, including distribution, ecology, and taxonomic notes, that is one of the more valuable parts of the book. Keys have been tailored to each genus and work very well. Primary keys to some genera (*Cyperus, Eleocharis*) and sections (*Carex* sect. *Bracteosae*) are geographical, while the majority are based on morphology. Keys for Carex are particularly effective. An extended discussion is provided for the notoriously difficult *Carex* section *Ovales,* which Boivin has divided into eight groups based on distinctive morphological features.

The figures are perhaps the weakest aspect of the book. The half-page figures showing from two to nine species provide good overall illustrations of inflorescences for all species, but often omit critical details of achenes, scales or perigynia. In particular, veins

or nerves are not clearly shown in these figures. The placement of figures is also poor, often separating related taxa or the description and illustration for a particular species. For example, *Fimbristylis* and *Bulbostylis,* two easily confused genera, appear on separate figures, as do the two species of *Scleria.* For *Carex nardina,* the text and figure are separated by fifteen pages. Although the illustrations have scale bars, it is not clear what measurements these represent.

Boivin's taxonomic approach is characteristically idiosyncratic. He frequently combines species, often to an extent greater than that of Cronquist (Gleason and Cronquist, 1991). As examples, *Scirpus longii* is reduced to *S. cyperinus* var. *brachypodus,* and *S. acutus* and *S. validus* are combined as *S. lacustris.* Many species of *Carex* sect. *Ovales* have been reduced to varietal status (*C. bicknellii* to *C. brevior* var. *crawei,* for example). Boivin makes significant use of the taxonomic rank of 'forma', and recognizes numerous nothospecies. Since it preserves Boivin's understanding of the family, this treatment does not recognize many recent taxonomic revisions in *Carex* and *Scirpus,* including several by the editorial team.

Despite some flaws, this volume is an excellent reference for botanists interested in the sedge flora of northeastern North America. Descriptions are clear and concise, the keys work well, and the discussions provide valuable habitat and taxonomic information. The taxonomic treatment provides an interesting alternative to other recent works, and may stimulate further research to resolve the conflicting opinions of two of the most notable floristic botanists of our time.

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THE ENVIRONMENT AND VASCULAR FLORA OF NORTHEASTERN IOWA FEN COMMUNITIES

JEFFREY C. NEKOLA

ABSTRACT

While fen communities have been long known from northwestern Iowa, only recently have they been found to occur in northeastern Iowa, south of the limit of Wisconsinan glaciation. Since 1984, over 2333 potential fen sites were surveyed in this region, and 160 were found extant. Extant fen sites can be divided into one of five classes dependent upon surficial geology: pre-Illinoian till, bedrock, eolian sand, fluvial sand, and oxbows. Five of eight soil chemistry variables differed significantly across these geologic classes, including organic matter, pH, available phosphorus, calcium, and magnesium. Soil pH, organic matter, and available magnesium were found to have fairly well-defined spatial gradients across northeastern Iowa fen sites. Four principal axes of climatic variation were also described from northeastern Iowa, and include temperature, precipitation, growing season, and summer precipitation. A total of 320 vascular plant taxa were located or have been reported from this community, with seven being only known from historical records. Fully 44% of the flora are considered rare in the region or state. Of these, 30% are rare in northeastern Iowa, 20% are rare in the state, 12% are listed for state legal protection, 11% are newly known from the northeastern Iowa flora, and 4% are newly known from the Iowa flora. Even though northeastern Iowa fens currently cover only .01% of the northeastern Iowa land surface, they contribute significantly to state and regional biodiversity by harboring approximately 28% of the regional and 18% of the total state flora.

Key Words: fens, Iowa flora, rare species, biodiversity

INTRODUCTION

Fens are peatland areas whose source water has been enriched in nutrients by passage through the ground (Sjörs, 1952; Moore and Bellamy, 1974). While covering a large extent of the boreal North American landscape (Horton et al., 1979; Glaser, 1987), along the glacial margin in North America fens are generally

Table 1. States in the eastern U.S. where fens have been reported.

State	Selected References
Connecticut	LeFor, 1986
Illinois	Sheviak, 1974
	Swink and Wilhelm, 1979
	Moran, 1981
Indiana	Friesner and Potzger, 1946
	Shuey, 1985
	Wilcox et al., 1986
Iowa	Anderson, 1943
	Nekola and Lammers, 1989
Kansas	Horr and McGregor, 1948
	Grüger, 1973
Massachusetts	Weatherby and Crow, 1992
Michigan	Cain and Slater, 1948
	Schwintzer, 1978
	Kron, 1989
Minnesota	Glaser, 1987
	Coffin and Pfannmuller, 1988
Missouri	Steyermark, 1938
	Orzell, 1983
	Nelson, 1985
Nebraska	Kaul et al., 1988
New Jersey	Breden and Smith, 1988
New York	Stewart and Merrell, 1937
	McVaugh, 1958
North Carolina	Schafale and Weakley, 1990
North Dakota	Seiler and Barker, 1985
	Malterer and Bluemle, 1988
Ohio	Gordon, 1933
	Andreas, 1985
	Stewart, 1987
Pennsylvania	Conard, 1952
	Breden and Smith, 1988
South Dakota	Over, 1932
	Ode, 1985
Virginia	Ogle, 1984, 1989
West Virginia	Hutton et al., 1968
	Bartgis and Lang, 1984
Wisconsin	Curtis, 1959
	Carpenter, 1990
	Reed, 1985

considered one of the rarest habitats in the landscape (Reed, 1985; Eggers and Reed, 1990). Fens or fen-like areas have been reported from a number of central and eastern states (Table 1), where they harbor a distinct flora including many rare species.

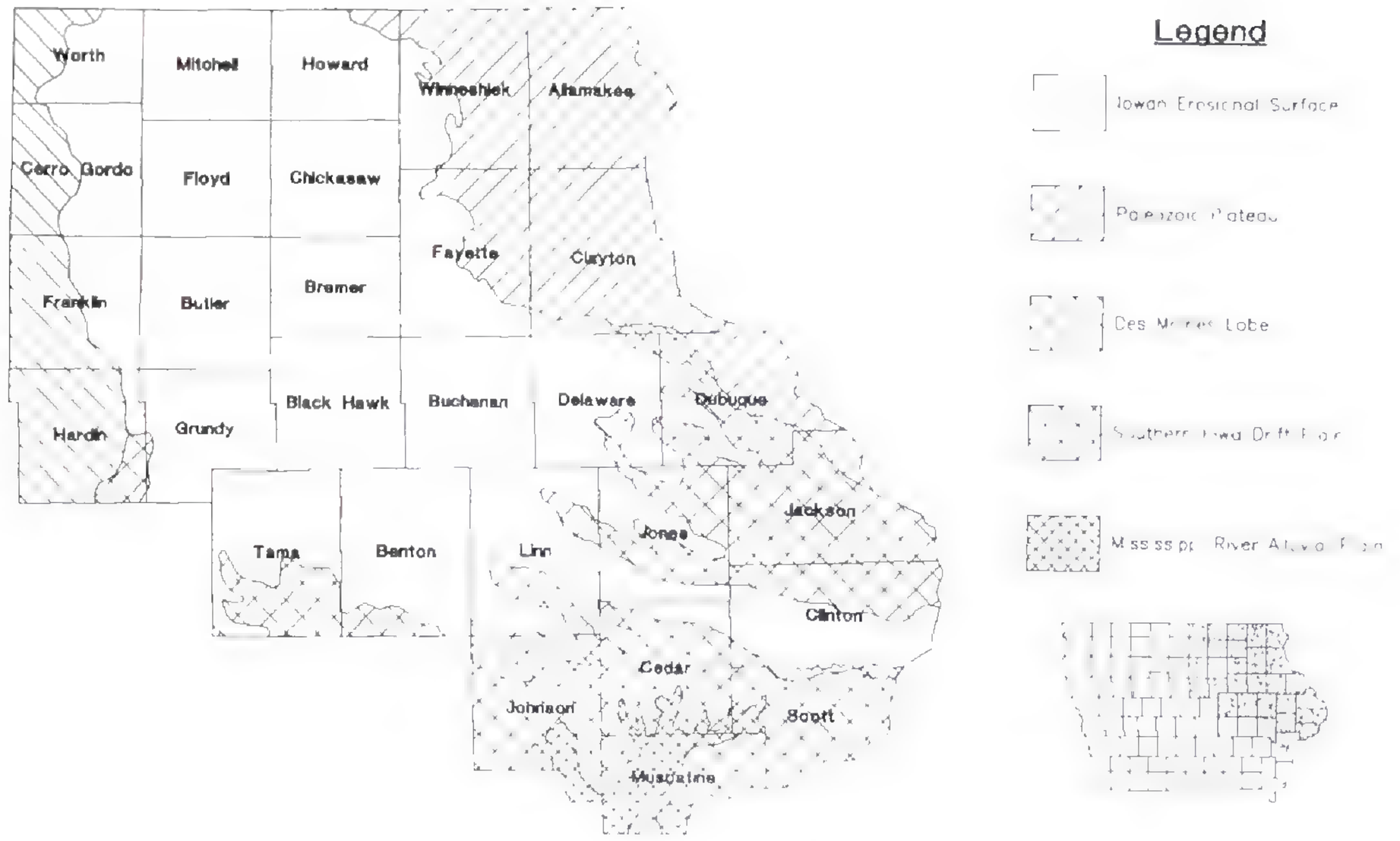

Figure 1. Landforms and counties included in the study region. Landform boundaries are based on Prior (1991).

Fens have long been the subject of research along the western side of the Wisconsinan terminal moraine in northwestern Iowa (Cratty, 1903; Wolden, 1926; Anderson, 1943; Hayden, 1943; Conard, 1952; Thorne, 1952; Holte and Thorne, 1962; Holte, 1966; van der Valk, 1975; Lammers and van der Valk, 1979; Moats, 1981). Until the mid-1980's biologists and ecologists thought that fens were restricted in Iowa to this region (e.g., Roosa and Eilers, 1978).

However, spring-fed, hillside peat deposits (termed 'mound springs') were also reported from northeastern Iowa in early geologic surveys (White, 1870; Calvin, 1897, 1902). These habitats remained biologically undescribed until 1984, when the flora of a northeastern Iowa site was studied (Nekola and Lammers, 1989). Like fens elsewhere in central and eastern North America, this site was found to harbor a large number of regionally rare species.

To better assess the regional fen environment across northeastern Iowa, and its contribution to local biodiversity, reconnaissance for all extant fen sites within the Iowan Erosional Surface, Paleozoic Plateau, and portions of the Southern Iowa Drift Plain and Mississippi River Alluvial Plain of Prior, 1991 (Figure 1) was conducted. Results from this survey will be used to address three main topics: (1) What was the original extent of fens in eastern Iowa, and how many remain extant? (2) What is the

environmental variation of the extant sites in terms of their underlying geology, soil chemistry, and regional climate? (3) What is the species diversity of these sites, and how do they contribute to state and regional biodiversity?

METHODS

A. Site Location

For purposes of this study, fens were defined as wetland areas with saturated but not inundated soils which are fed by permanent groundwater seepage. This definition differs slightly from those typically used by European researchers (e.g., Sjörs, 1952; Moore and Bellamy, 1974) in that sites which have saturated soils, but little or no peat accumulation are considered fens. The broader definition of 'fen' used in this study follows the precedent of many other U.S. fen researchers (e.g., Holte, 1966; Andreas, 1985; Weatherbee and Crow, 1992).

Potential fen sites in northeastern Iowa were located through use of county soil survey maps prepared by the USDA Soil Conservation Service (SCS). These modern soil survey maps have been completed for all counties within the study region. The location of potential sites was made possible as most occurrences of muck or peat soils (variously named 'Peat', 'Muck', 'Palms Muck', or 'Houghton Muck') are restricted to fen sites.

From 1984 to 1991 all occurrences of peat soil pedons occurring on SCS county soil maps in the 29-county study region were visited to determine the location of extant sites. Sites were considered extant if they possessed essentially undisturbed vegetation and/or rare species. A number of undrained sites that had been completely invaded by weedy plants such as *Phalaris arundinacea,* or had been grazed beyond recognition, were excluded from this list. The boundaries of all pedons of fen soil mapped by the Soil Conservation Service were digitized to provide a regional perspective on the distribution of presettlement and extant sites.

B. Soil Analysis

Four soil samples were collected from each extant fen in an attempt to capture the range of soil variation present. These samples were oven dried, and 50 g taken from each to make a single

composite sample for each site. Determination of percent organic matter, pH, NO_3-N, extractable P, exchangeable K, extractable SO_4-S, exchangeable Ca, and exchangeable Mg in these samples were conducted by Minnesota Valley Testing Laboratory of Nevada, Iowa, and followed the methodology of Dahnke (1988). These variables are referred to as percent organic matter, pH, P, K, S, Ca, and Mg, respectively, in the remainder of the paper. Water samples were not taken as standing water was not present at all sites, and as water samples could not be stored for later analysis. However, soil and water chemistry should covary as any dissolved or suspended particulates will remain in the soil after drying.

One-way ANOVA's were used to test the significance of differences for these soil variables across five classes of underlying surficial geology. An approximation of the spatial distribution of each variable across northeastern Iowa fen sites was estimated through the interpolation technique of block kriging (Burgess and Webster, 1980).

C. Climatic Analysis

Twenty-two climatic variables were calculated as 30-year means from 96 recording stations across Iowa. Principal components analysis was conducted on all variables to identify the most important axes of variation. These axes were related to the original variables through use of a vari-max rotation. To document the spatial distribution of each of these four main axes within the study region, the interpolation technique of block kriging was used to estimate the variation of each across the study region.

D. Floristic Analysis

Occurrence of all vascular plant species were noted for all extant northeastern Iowa fens. In addition, a survey was made of the northeastern Iowa botanical literature (Fitzpatrick, 1899; Barnes et al., 1900; Pammel, 1908; Guldner, 1960; Cooperrider, 1962; Hartley, 1966; Eilers, 1971) to identify all species that were historically known from these habitats but for which no extant populations could be located.

Five types of rarity within the flora were assessed. First, rarity

within northeastern Iowa is based on classifications provided from the two regional floras (Cooperrider, 1962; Eilers, 1971) whose boundaries fall entirely within the region of this current study. For a taxon to be considered rare within the region, it had to be considered either rare in both of these floras, or rare in one and absent from the other. Second, state-level rarity was assessed following Howe et al. (1984). Third, the listing of the taxa legally designated as 'Endangered', 'Threatened', and 'Special Concern' in Iowa was based on Roosa et al. (1989). Fourth, taxa new to the regional flora are based on Guldner (1960), Cooperrider (1962), and Eilers (1971). Lastly, the designation of taxa new to the state is based on those not found in published county and regional floras.

Voucher collections were made for all rare taxa occurrences by top-snatching relevant material so that populations would not be affected. Specimens were deposited at the R. V. Drexler Herbarium at Coe College, Cedar Rapids, Iowa. Where populations were large enough, duplicate specimens were also made and placed in the University of Iowa Herbarium, Iowa City, and the University of North Carolina Herbarium, Chapel Hill.

RESULTS AND DISCUSSION

A. Distribution of Presettlement and Extant Sites

In total, 2333 potential sites were identified from SCS soil maps in the 29 eastern Iowa counties surveyed (Figure 2a). Of these, only 160 remained extant by 1991 (Figure 2b). Site names, sizes, geologic class, and locations for these sites are given in Appendix I.

In presettlement, clustering of fen sites was present at a number of differing spatial scales. At a regional scale, sites clustered into two general groups: one paralleling the eastern margin of the Des Moines Lobe, and the other paralleling the eastern border of the Iowan Erosional Surface.

At smaller scales (approximately the size of counties), roughly parallel northwest-to-southeast trending bands of high site density

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Figure 2. Distribution of fen habitats in northeastern Iowa, based upon digitization of SCS county soil maps. a: Presettlement. b: 1991.

Figure 2a: Presettlement Fens

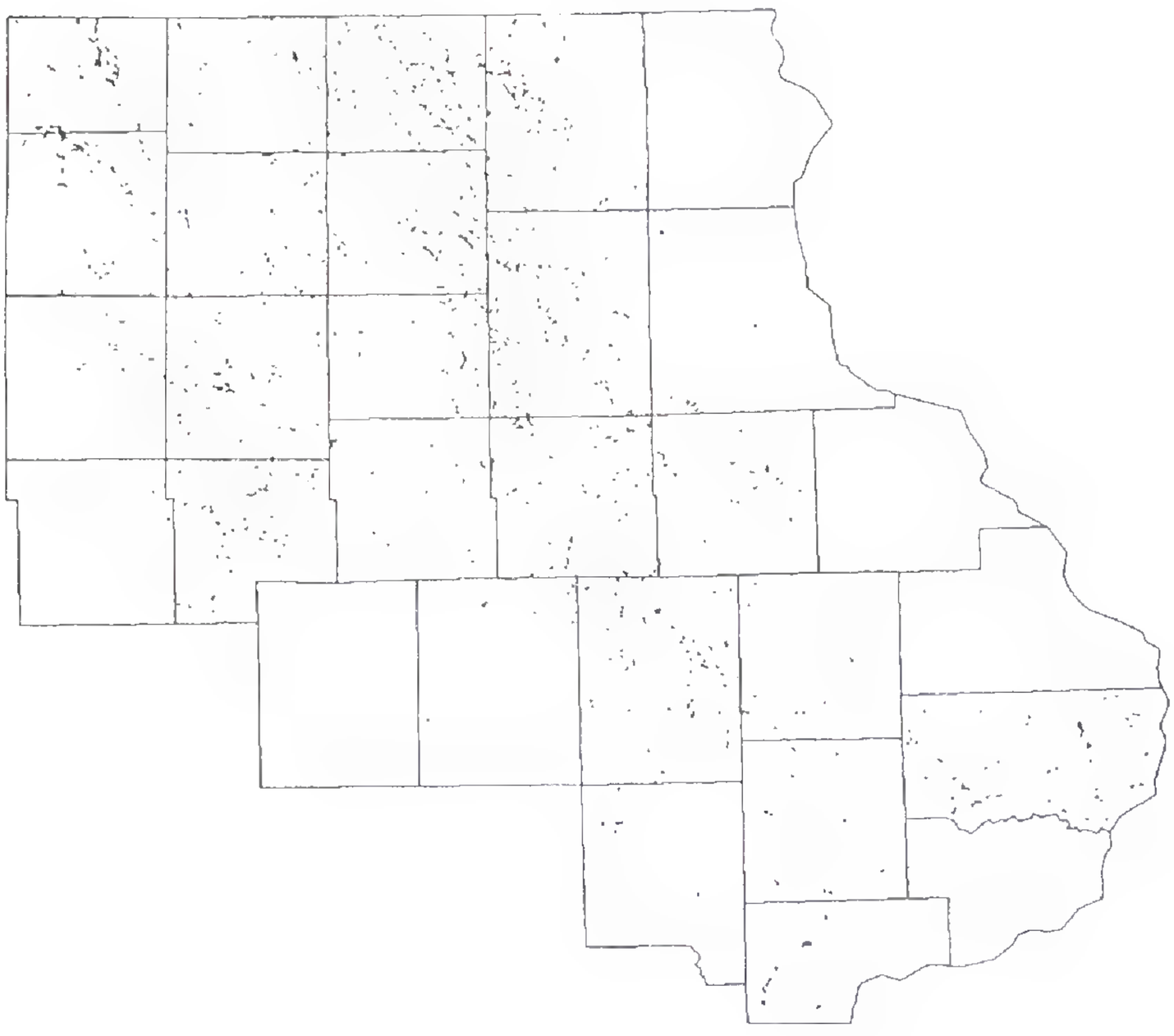
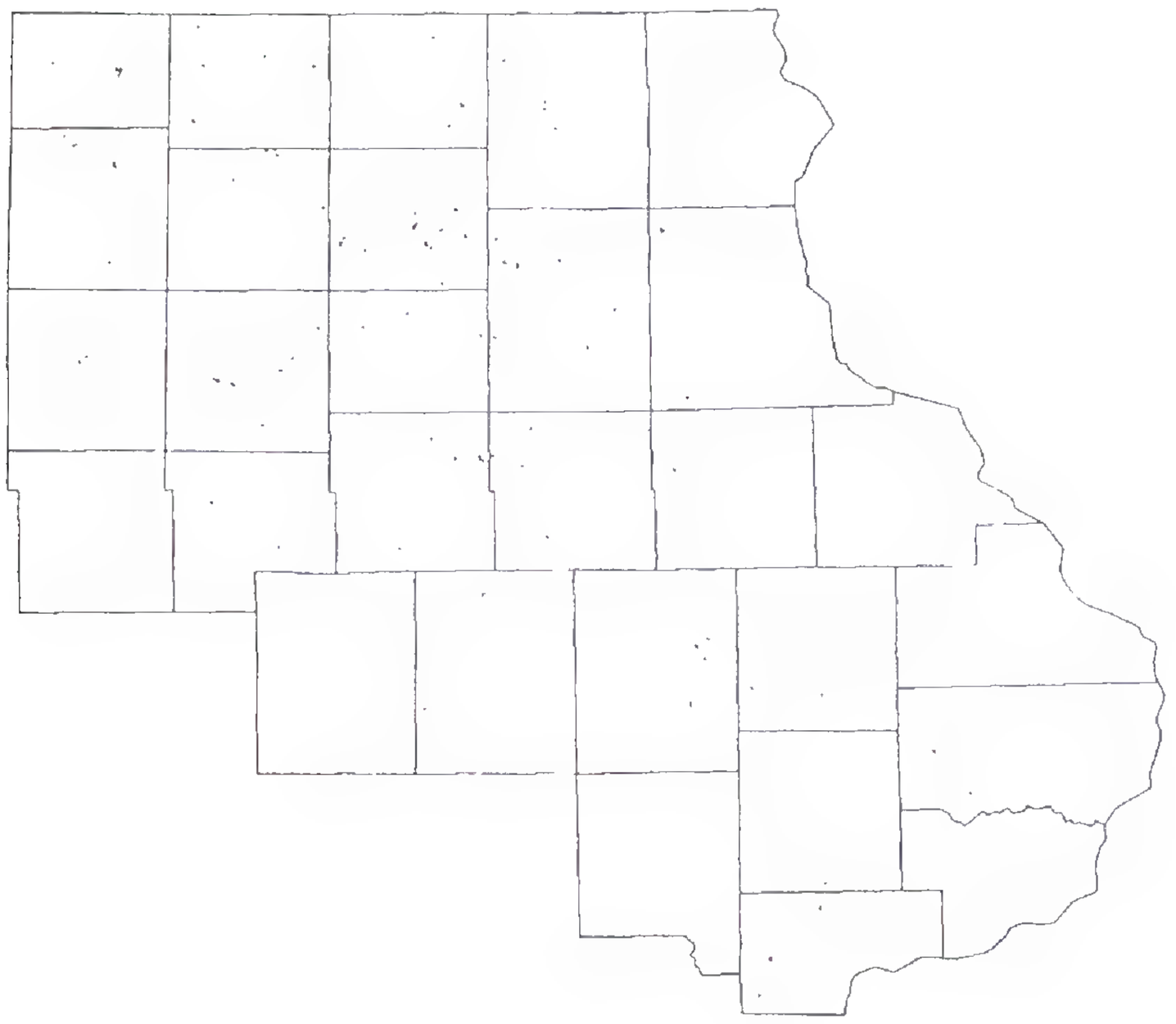


Figure 2b: Extant Fens - 1991



approximately 10–15 miles wide and 75 miles long occurred. In the western cluster, these bands seem to be closely related to outwash sands and gravels along the Winnebago and Shell Rock Rivers. In the east, longer and more diffuse bands are present which seem to cut across local drainage patterns and topography. One of the most marked of these concentrations begins in central Chickasaw County and terminates in northwestern Cedar County. It is possible that these bands of high site density correlate with locations of pre-Illinoian moraines where the concentration of upland gravel deposits are greater.

At even smaller spatial scales (roughly the size of a township) individual sites were often grouped into linear strings. The most intriguing of these are a parallel series of five such strings which extend over a 30 mile extent in Chickasaw, Howard, Fayette, and Winneshiek Counties. The underlying factors responsible for such pattern are not known.

While diverse spatial structure existed in presettlement site distribution, the loss of 93% of sites in the last 50–100 years has led to the destruction of almost all of this pattern. The distribution of extant sites now appears almost random, with even the large regional clusters being almost unidentifiable. This loss of spatial structure will probably lead to a decrease in the rate of immigration between sites, and alter the direction of species migration through the landscape.

SCS maps, which were used to generate these data, should not be considered infallible sources of information. Two caveats regarding their use in documentation of presettlement fen sites must be made. First, not all fen sites present in the presettlement landscape have been mapped. This form of error has led to the exclusion of some historic and extant sites from the published soil maps. For instance, a site near Tipton described by White (1870) is not mapped in the Cedar County soil survey. Also, eleven percent of the extant sites listed in Appendix I were not mapped as possessing fen soil pedons, and were located by visual inspection during field reconnaissance or from local contacts.

The second form of error in soil survey mapping of potential fen sites occurs when marsh habitats with peat accumulations are mapped as possessing soils characteristic of fen sites. Although such wetlands may have muck or peat soils, they do not provide proper habitat for fen species, and do not represent potential fen habitats. The mapping of all muck soil pedons in such cases will

overestimate the number of presettlement fen sites. This error is most prevalent in the western counties bordering the Des Moines Lobe, where numerous pothole marshes with peat accumulations were present prior to draining. Some of the mapped areas of peat or muck soil in Clinton County may also represent former marsh habitats. This form of error was minimized by only digitizing sloping, hillside peat pedons on the Des Moines Lobe, thereby removing potential marsh habitats from analysis. As it was not possible to make any *a priori* rules for exclusion of potential Clinton County marsh sites, all peat pedons in that county were mapped. However, field observations suggest that less than 10% of potential Clinton County sites represent former marsh sites, indicating a relatively low rate of this form of error.

Although county soil maps represent an imperfect data source, they are the best and only estimate available of the presettlement extent of fens in northeastern Iowa. As both of these error rates are relatively low (approximately 10%), the analysis presented above should thus reflect the trends in site distribution once present in presettlement landscape.

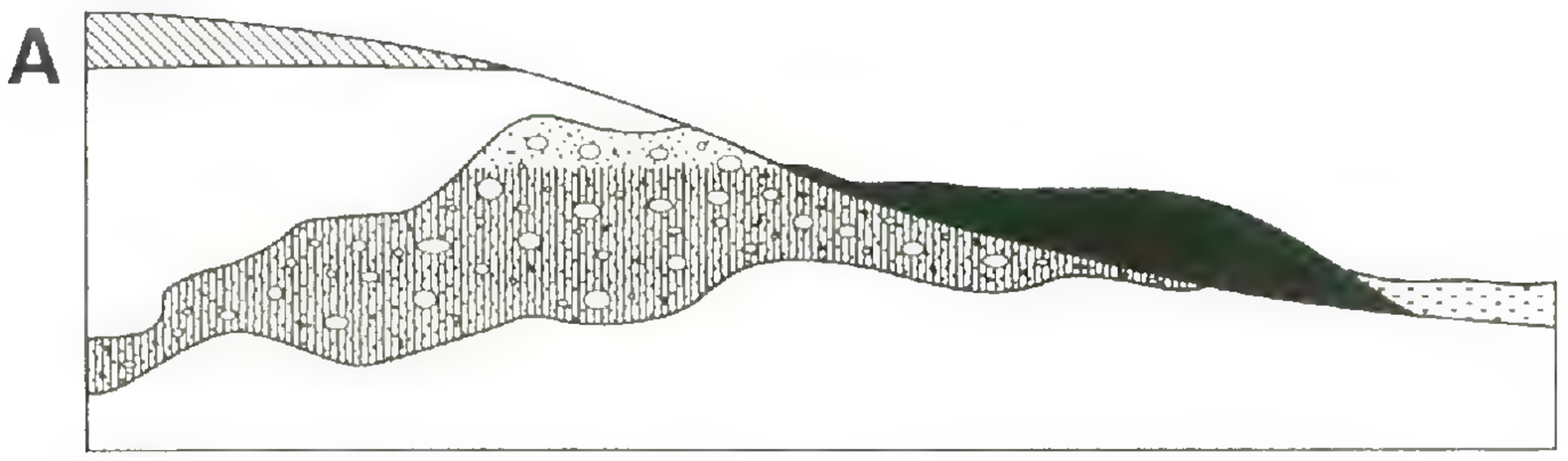
B. Environmental Variation Across Northeastern Iowa Fen Sites

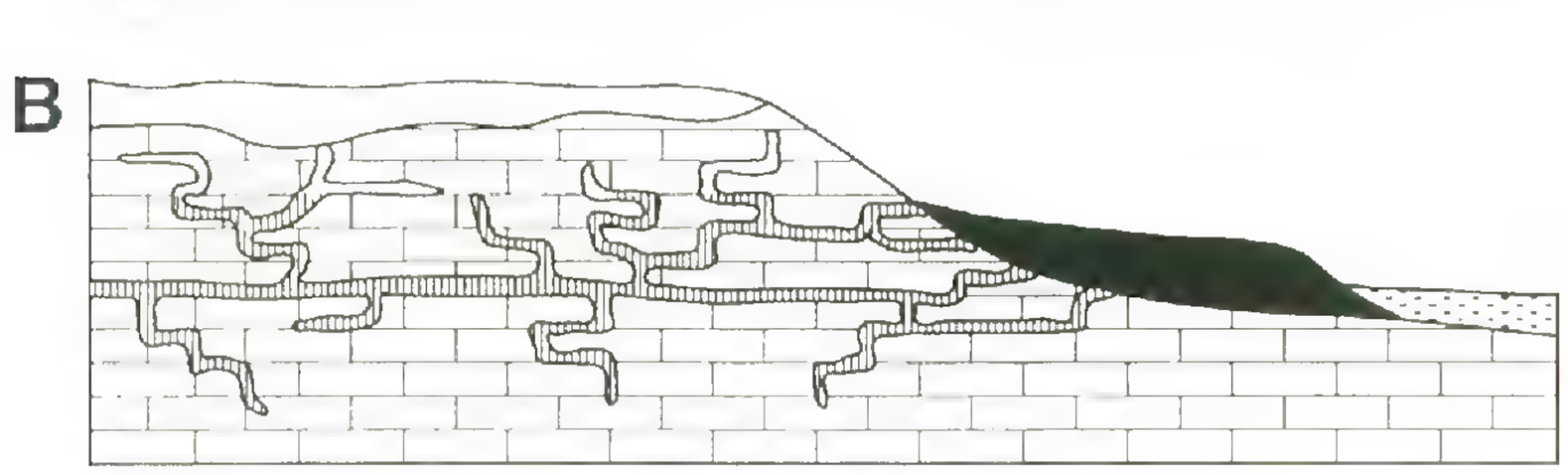
Geologic Classification

The majority of the region included in this study was unglaciated during the Wisconsinan and subjected to intense periglacial erosion which removed existing tills and exposed water-bearing till or bedrock sequences, created stepped landscape surfaces, and prevented deep accumulations of loess (Hallberg et al., 1978; Prior, 1991). The sediment liberated through periglacial erosion was deposited as eolian and fluvial sands along major river corridors (Prior, 1991).

Depth of loess accumulation appears to negatively covary with abundance of fen sites. On the southern margin of the study region in Tama, Benton, Cedar, and southern Linn Counties where periglacial erosion was less intense and loess deposits accumulated (Anderson, 1983), fens are much less frequent than in the till-mantled or bedrock-controlled landscapes to the north which experienced higher erosion rates.

The 160 extant fens in northeastern Iowa were classified into


A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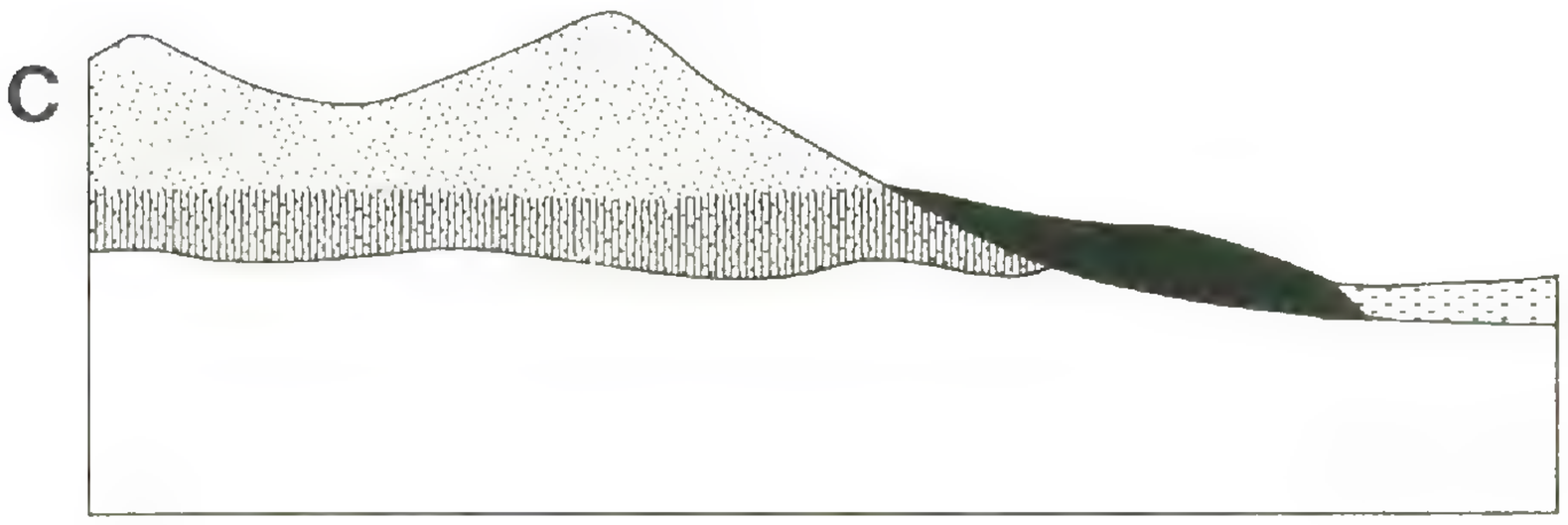
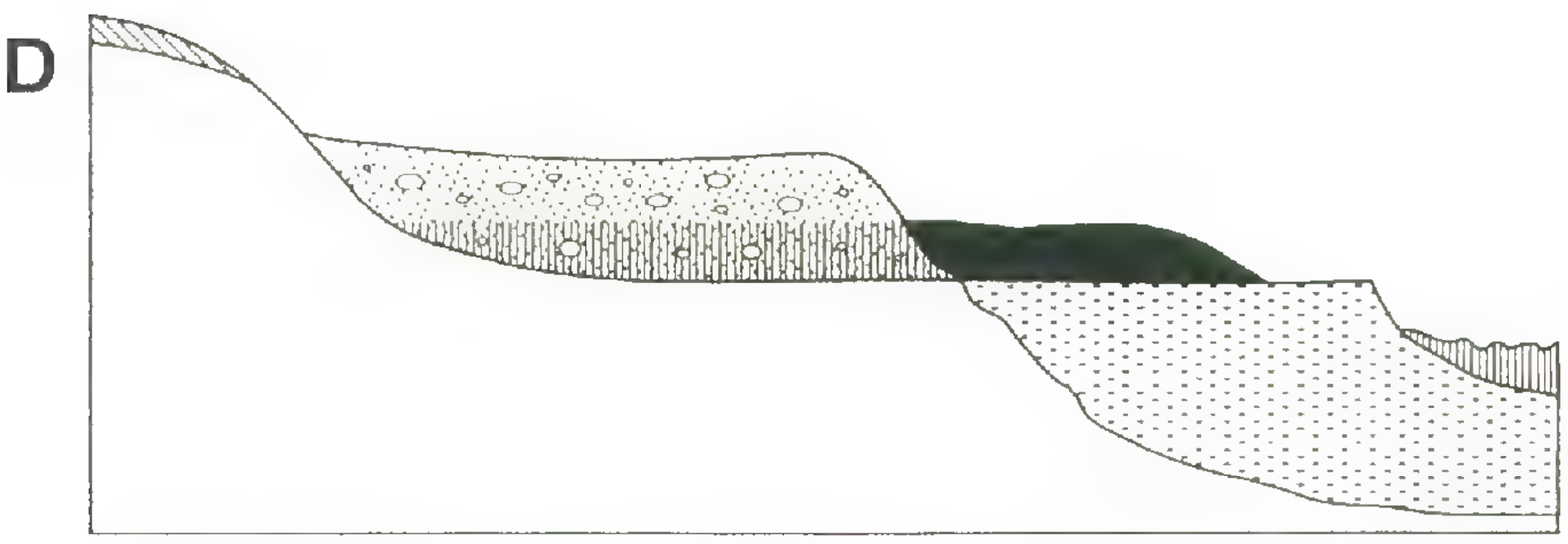

C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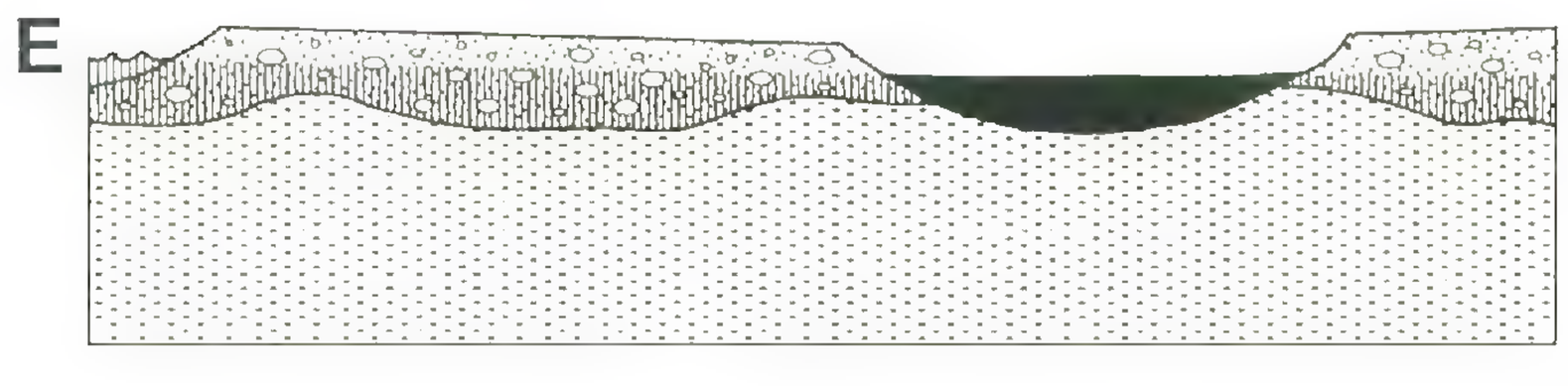
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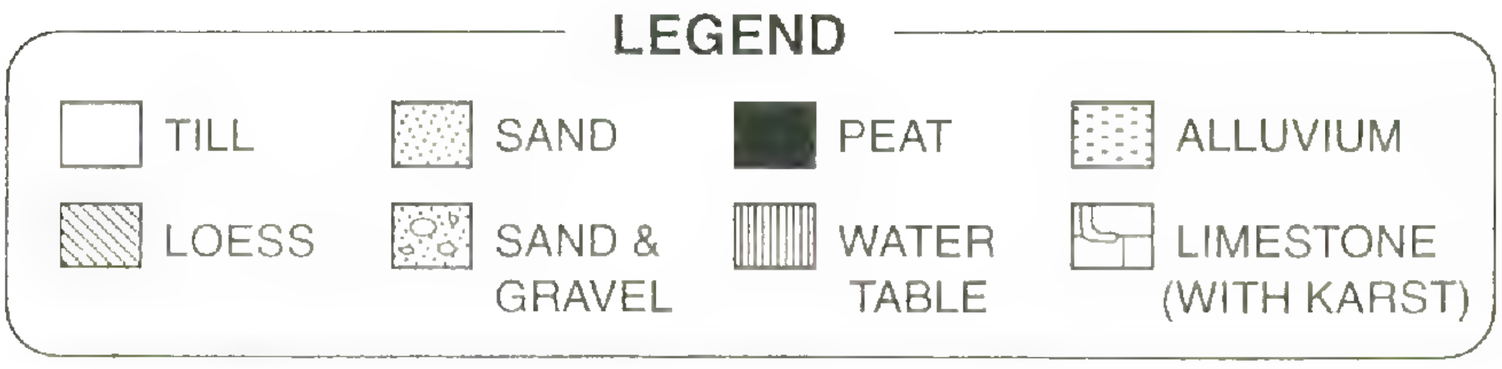
LEGEND
TILL
SAND
PEAT
ALLUVIUM
LOESS
SAND & GRAVEL
WATER TABLE
LIMESTONE (WITH KARST)

five broad groups based upon their underlying geology: pre-Illinoian till, bedrock, eolian sands, fluvial sands, and oxbows. These groups basically follow those of Thompson (1992) and Thompson et al. (1992), with the exception that (1) 'gravel ridge' sites have not been separated from other pre-Illinoian till sites as they simply represent pre-Illinoian till sites occurring in a more eroded landscape, and (2) sites developed in upland, eolian sands have been differentiated from those found with fluvially-deposited sands and gravels.

The most frequent geologic class of northeastern Iowa fens is associated with deposits of pre-Illinoian sand and gravel (Figure 3A). These 119 sites are found throughout the region (Figure 4) in association with water-bearing gravels deposited within and between tills (Thompson, 1992). The majority of pre-Illinoian till fens are found on footslopes along pediment margins (Hallberg et al., 1978), although they may occur at any position in the landscape where water-bearing gravels have been exposed.

Fens associated with bedrock aquifers (Figure 3B) are much less frequent (13 sites), and are restricted to the northeastern and northwestern parts of the study region (Figure 4) where most or all of the till was removed through periglacial processes. Like pre-Illinoian sites, bedrock fens are usually found on footslopes along pediment edges. While peat usually has formed in these fens, some sites have only minor peat accumulations, and have a soil surface consisting of cold, wet, limestone rubble. Such sites contain some of the most calcareous fen habitats found in the region.

Fens associated with eolian sands (14 sites) are restricted to the southern third of the region, with the majority being found along the Wapsipinicon and Cedar Rivers where extensive dune fields have formed in the surrounding uplands (Figure 4). Some eolian sand sites are also found along sand-mantled paha ridges distant from rivers (for an explanation of pahas see Prior, 1991). Eolian sand fens are often found along the base of dunes where the downward flow of water is stopped by more impervious tills or paleosols (Figure 3C). Many of these sites contain relatively low

←

Figure 3. Idealized cross-section diagrams of the five classes of northeastern Iowa fens based on surficial geology. a: Pre-Illinoian till; b: Bedrock; c: Eolian Sand; d: Fluvial Sand; e: Oxbow.

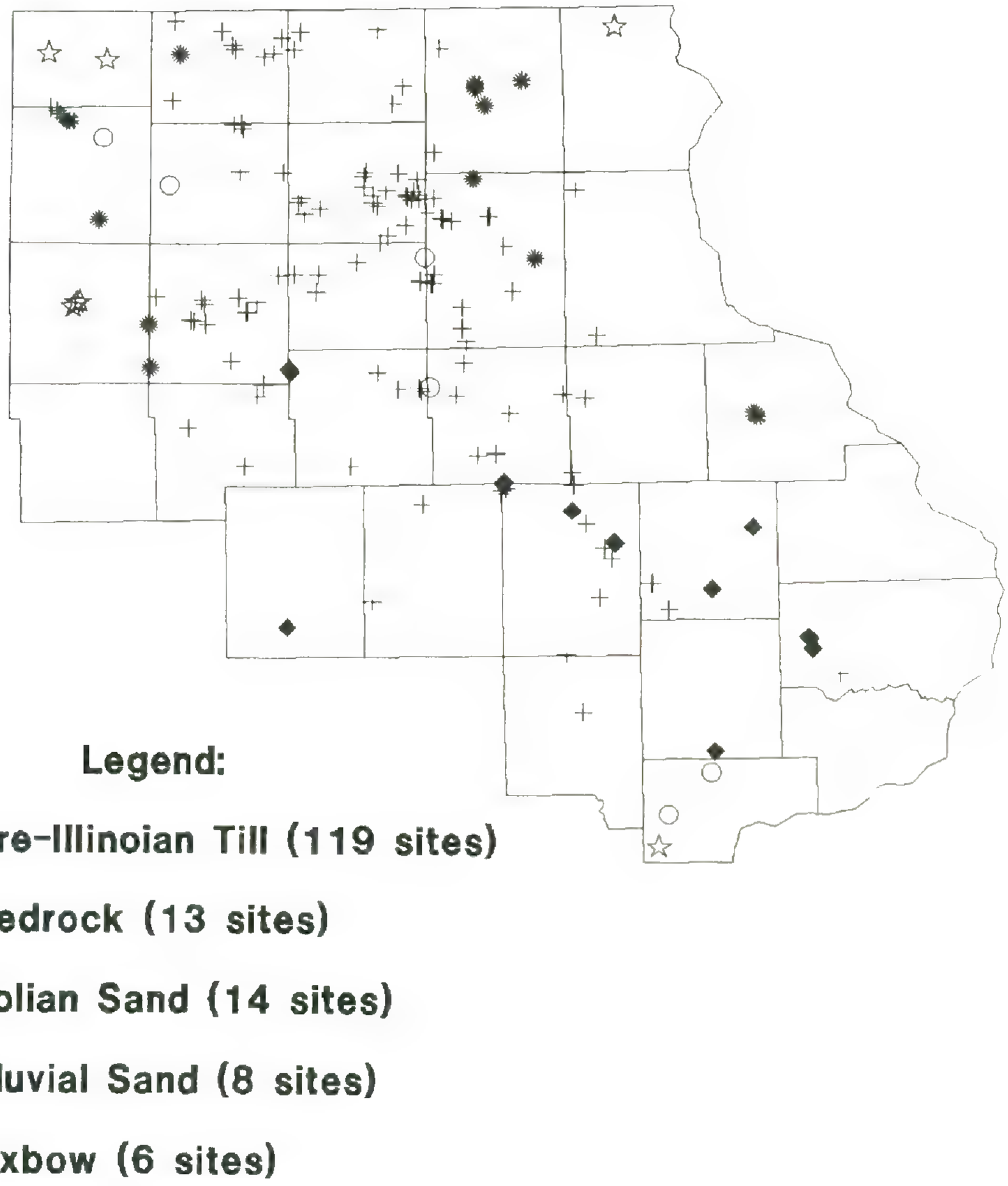

Figure 4. Distribution of the five geologic classes of northeastern Iowa fens.

amounts of organic matter and have margins consisting of wet, acidic sands. The lowest percent organic matter, pH, Ca, and Mg readings from eastern Iowa fens occur in these sites (see below).

Fens associated with fluvial sand and gravel terraces are rarer yet (8 sites). Fluvial sand fens occur when water moving through sands and gravels emerges to the surface along terrace margins (Figure 3D). While most of these sites are associated with outwash sands and gravels along the western section of the study region, three sites were found along the Upper Iowa and Cedar Rivers in Allamakee and Muscatine Counties (Figure 4). The largest single presettlement sites identified in the region by SCS maps occurred with fluvial sand and gravels along the Shell Rock and

Winnebago Rivers. Only a small part of a single one of these sites remained extant by 1991. Floristic lists from these sites prior to draining (Pammel, 1908, 1917) suggest that they once contained one of the most diverse fen floras in the state.

The most uncommon type of fen in northeastern Iowa are those formed from hydric succession of oxbow channels along abandoned stream meanders (6 sites). While oxbow channels typically have open water and would not support fen species, organic matter accumulation can continue until the soil surface becomes equivalent to the water table, creating the saturated but not inundated conditions necessary for colonization of fen species (Figure 3E). Fens occupying former oxbow channels are scattered throughout northeastern Iowa along the Winnebago, Cedar, Wapsipinicon, and Little Wapsipinicon Rivers (Figure 4). The greatest concentration of this fen type once occurred along the Cedar River south of Iowa City in the 'Lake Calvin Basin' where a number of successive oxbow lakes have formed fen habitats. Baker et al. (1987) have characterized the Holocene history of one of these sites through macrofossil and pollen analysis.

Geologic History

The landscapes upon which northeastern Iowa fens are found have formed through erosional processes within the last 20,000 years. The age of fen sites in this landscape was investigated by Thompson (1992), who determined the dates of the basal peat layer, using C_{14} isotope analysis, for ten sites. The age of basal peats in each of these sites were found to differ greatly, ranging between 10,900 and 2280 years B.P.

The interpretation of these dates is made more difficult by interruptions in peat deposition (sometimes accompanied by oxidized peat) within sites having the oldest basal dates (Hall, 1971; Van Zant and Hallberg, 1976). Fens without old (8000 year) basal peat dates are underlain by oxidized clay, till, or occasionally prairie soil (J. C. Nekola and R. G. Baker, unpubl. data). The existence of oxidized layers of peat or mineral soil underlying fen sites suggests that prior to modern peat development the site dried out, exposing the peats and underlying substrates to oxidation and erosion.

Fens in northeastern Iowa thus appear to be a Holocene phe-

Table 2. Comparison of means and standard deviations from soil chemistry variables between all surficial geology groups, and over all sites. Standard deviations are presented within parentheses under the mean for each group.

	Geologic Group					
Variable	Pre-Illinoian Till	Bedrock	Eolian Sand	Fluvial Sand	Oxbows	All
% Organic	40.9 (12.3)	26.5 (13.2)	18.8 (16.2)	29.1 (7.8)	35.5 (15.4)	37.0 (14.5)
pH	6.2 (.5)	6.6 (.6)	5.4 (.7)	6.8 (.3)	5.8 (.7)	6.2 (.6)
N	1.1 (1.3)	0.7 (.4)	0.8 (.6)	0.6 (.4)	0.6 (.3)	1.0 (1.7)
P	26.6 (14.6)	20.9 (15.8)	37.6 (13.1)	10.6 (9.2)	29.0 (13.0)	26.5 (15.0)
K	42.2 (17.6)	47.6 (23.6)	44.4 (22.6)	42.7 (7.4)	42.2 (18.9)	42.9 (18.2)
S	186.4 (140.1)	208.1 (159.7)	100.6 (69.7)	126.0 (78.9)	195.7 (98.7)	178.4 (135.2)
Ca	4494.4 (923.8)	4364.8 (996.1)	2101.1 (1038.1)	4507.1 (827.9)	3331.4 (1176.2)	4224.1 (1168.9)
Mg	411.2 (130.6)	560.5 (146.9)	220.7 (92.8)	480.1 (119.7)	339.9 (129.2)	406.6 (146.9)

nomenon, with the onset of development generally coinciding with the end of the Hypsithermal (Thompson, 1992). The creation of new sites has apparently continued until present, with some bedrock and eolian sand sites having less than eight cm of peat accumulation. A similar pattern has been found in the boreal fens

Table 3. Summary statistics from a 1-way ANOVA comparing the differences in soil chemistry variables across all geologic classes.

Soil Variable	*P*	r^2
% Organic	.000	.261
pH	.000	.210
N	.433	.024
P	.001	.110
K	.813	.010
S	.133	.044
Ca	.000	.345
Mg	.000	.238

of central Canada (Zoltai and Vitt, 1990) and pocosins of the southeastern Coastal plain (Daniel, 1981).

The implication for this post-Hypsithermal development of fen sites is that rare species which are found on them cannot be postulated to represent Pleistocene relicts. Rather, all of the rare taxa found in this community have had to disperse into this landscape within the last 6000 years.

Soil Chemistry

Variation of soil chemistry as a function of geology

The mean and standard deviation for eight soil chemistry variables within each of the five geologic classes of fens are presented in Table 2. The results of one-way ANOVA's on each of these variables (Table 3) demonstrate that three variables (N, K, and S) show no significant differences between the five geologic groups. The remaining five variables (percent organic matter, pH, P, Ca, and Mg) were found to possess significant differences across the geologic groups. Organic matter was highest in pre-Illinoian and oxbow fens, and was lowest in sites developed in eolian sands. Soil pH was highest on sites developed on bedrock and fluvial terrace sands, and was lowest in eolian sand and oxbow sites. Phosphorus content was highest in eolian sand and oxbow sites, and lowest in fluvial sand and bedrock sites. Calcium concentration was highest in pre-Illinoian till and bedrock sites, and was lowest in eolian sand sites. Lastly, soil magnesium was highest in bedrock sites, and was lowest in eolian sand sites.

Although significant differences were observed in the central tendency of values for these soil chemistry variables between geologic groups, this should not imply that there is little overlap between the soil chemistry variables for sites in differing geologic groups. For instance, while the mean percent organic matter of pre-Illinoian till sites was twice that of eolian sand fens (Table 3), 75% of sites in these two groups have soil Ca found in the range between the lowest recorded pre-Illinoian till (1900 ppm) and highest recorded eolian sand (4000 ppm) values. This fact is also demonstrated in the r^2 values for the significant ANOVA's which ranged between 11% for P to 35% for Ca, implying that

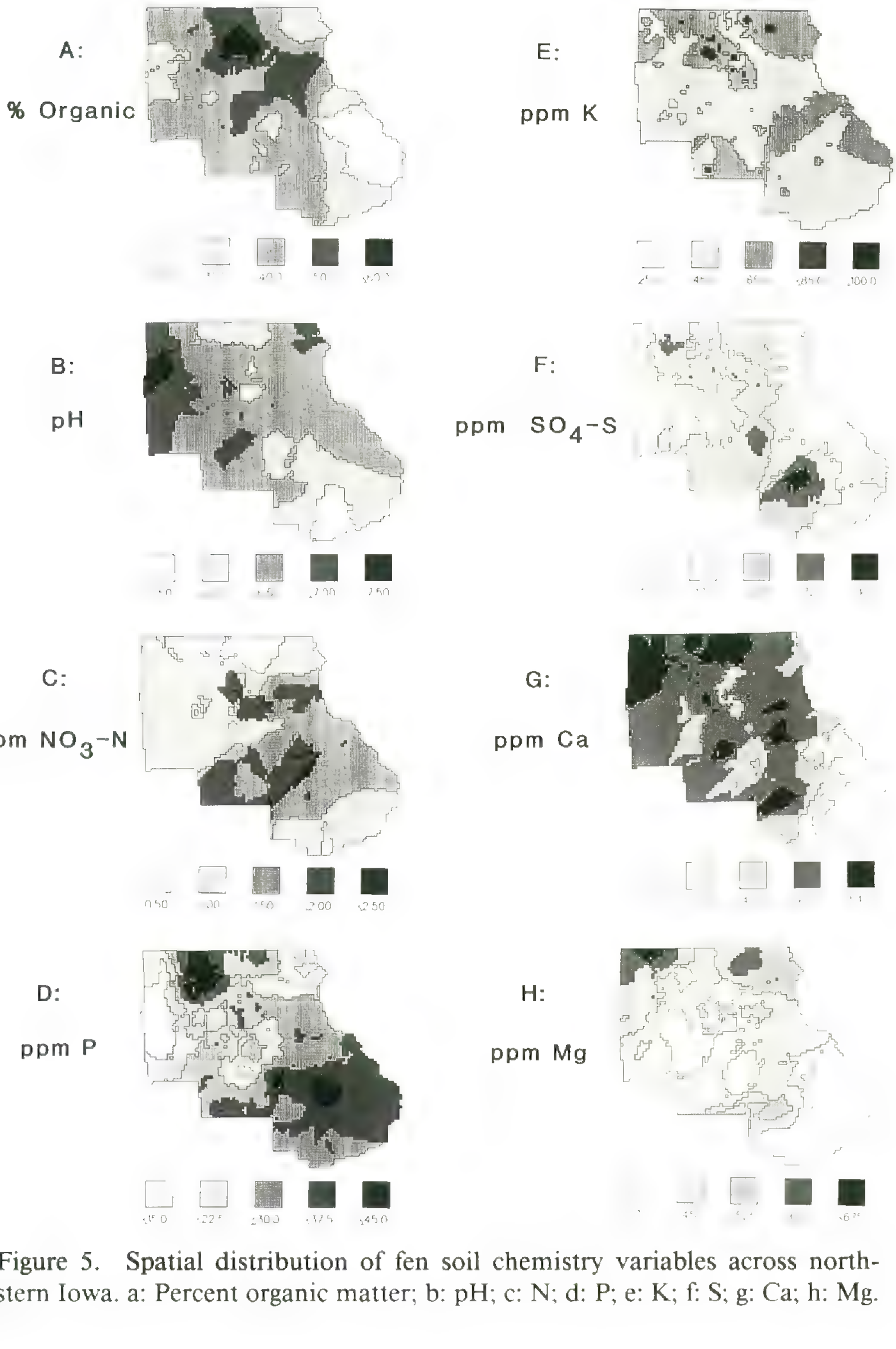

Figure 5. Spatial distribution of fen soil chemistry variables across northeastern Iowa. a: Percent organic matter; b: pH; c: N; d: P; e: K; f: S; g: Ca; h: Mg.

no more than ⅓ of the observed variance in these variables can be accounted for by geologic grouping. Thus, although the average for percent organic matter, pH, P, Ca, and Mg differ significantly between the geologic groups, the values overlap enough to make

it likely that any two sites will possess similar soil chemistry variables, independent of their surficial geology.

Variation in soil chemistry as a function of spatial location

How does soil chemistry vary in fen sites across the region? To address this question, kriged response surfaces for each of the eight soil variables were calculated for the study region (Figures 5A–5H). Relatively simple, approximately monotonic response surfaces were observed only in pH, organic matter, and Mg. The remaining soil chemistry variables have less clear spatial gradients as they possess multiple maxima and minima over the study region. The causes of all these gradients are undoubtedly complex, and related to climatic patterns (see below), and the non-random distribution of fens of differing geologic origin.

Climate

A final major class of environmental variation which defines the northeastern Iowa fen environment is climate, which will not only affect the distribution of species, but may also influence soil chemistry and the size and nature of groundwater aquifers.

Four major trends in climatic variation were identified over the study region through principal components analysis, accounting for 96% of the total variation. The first axis is related to temperature, and is most closely correlated with Average Yearly, Summer, Fall, and Spring Temperatures, Heat Stress Days/Year, Heat Stress Degrees/Year, Heating Degree Days, Cooling Degree Days, and Growing Degree Days. The variation of precipitation, exclusive of the summer months, represents a second major axis of variation. This axis is most closely correlated with Average Yearly, Winter, Spring and Fall Precipitation, Average Winter Temperature, and Maximum 24-hour Precipitation. The third major axis of climatic variation is represented by growing season, which is most closely correlated to 32°, 30°, 28°, 26°, and 24° Growing Seasons (in degrees Fahrenheit), and number of Freezing Days/Year. The last major climatic gradient is represented by Average Summer Precipitation. The spatial variation of each of these axes across the region was estimated by mapping the variable most highly correlated to each axis through block kriging (Figure 6A–6D).

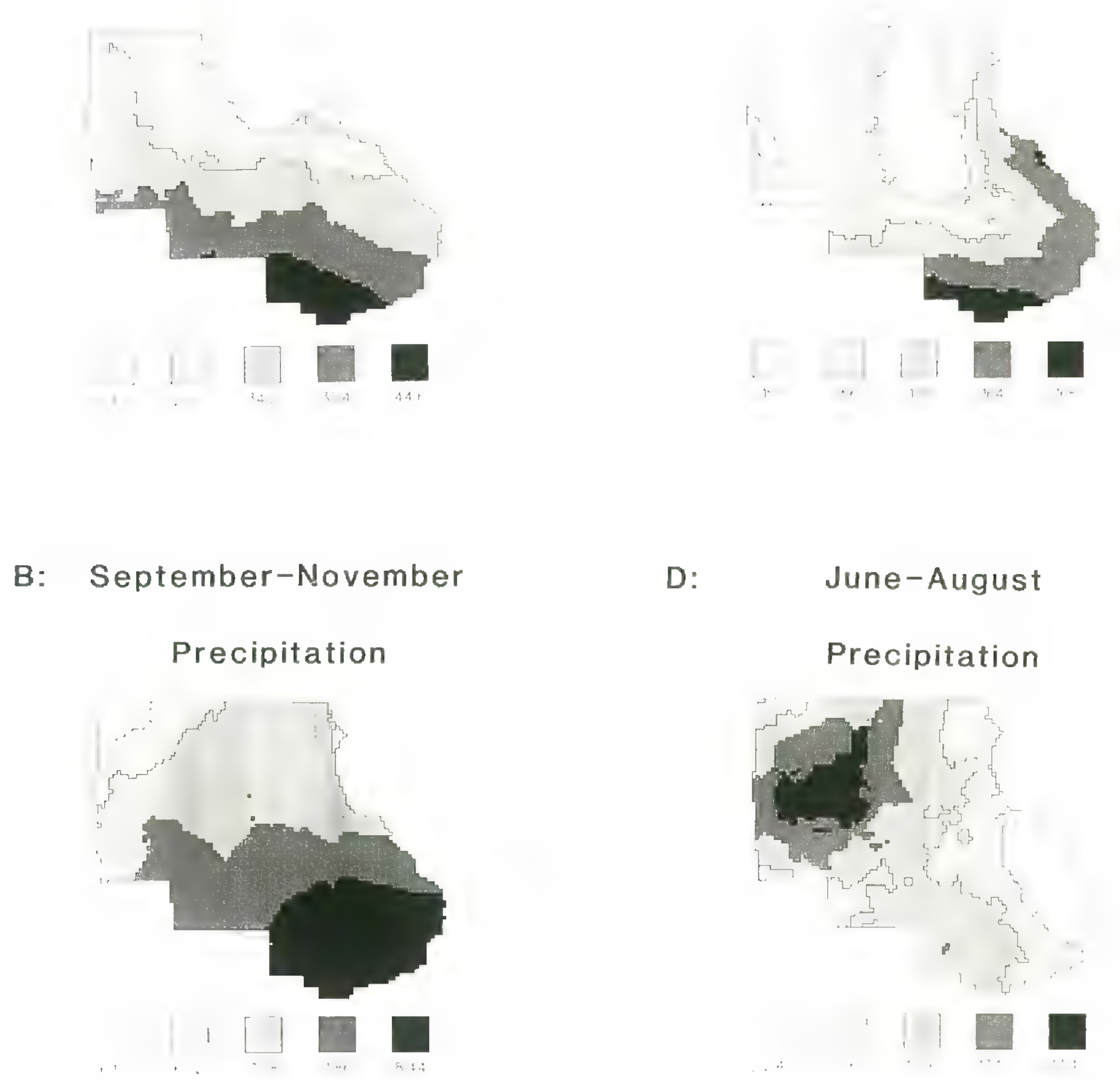

Figure 6. Spatial distribution of the main axes of climatic variation across northeastern Iowa, as represented by the variable most highly correlated with each axis. a: Temperature (as shown by Heat Stress Day/Year). b: Non-summer Precipitation (as shown by average fall (September–November) precipitation/year). c: Growing season (as shown by 32°F growing season). d: Summer (June–August) precipitation/year.

C. Biological Diversity of Northeastern Iowa Fen Habitats

Enumeration of the Vascular Flora

A total of 320 vascular plant taxa were recorded from northeastern Iowa fen communities (Appendix II). The flora includes approximately 23% which are incidental; their presence on fens

Table 4. Summary of the northeastern Iowa fen vascular plant flora in terms of major phylogenetic groups.

Division	Native Taxa			Exotic Taxa		
	Fen	Incid.	Tot.	Fen	Incid.	Tot.
Pteridophytes	10	5	15	0	0	0
Gymnosperms	0	1	1	0	0	0
Dicotyledons	145	49	194	4	4	8
Monocotyledons	84	13	97	3	2	5
Totals	239	68	307	7	6	13
Grand total						320

may be due to the mass effect (Shmida and Wilson, 1985) of surrounding communities. Only 13 taxa are exotic to northeastern Iowa, and almost half of these are incidental (Table 4). None of the exotic taxa at present is a threat to overall biodiversity on undisturbed sites, although some do invade disturbed areas.

The majority of the fen flora are dicotyledons, followed by monocotyledons, pteridophytes, and gymnosperms (Table 4). Of the families present in the fen flora, the two largest (in terms of taxa represented) are the Compositae and Cyperaceae, followed by the Gramineae, Salicaceae, Rosaceae, Labiatae, and Orchidaceae (Table 6). The best represented genera are *Carex, Salix, Aster, Cypripedium,* and *Solidago* (Table 5).

Table 5. Enumeration of the largest families and genera present in the northeastern Iowa fen vascular plant flora.

Families (7 or more taxa)		Genera (5 or more taxa)	
Name	Number of Taxa	Name	Number of Taxa
Compositae	41	*Carex*	27
Cyperaceae	40	*Salix*	14
Gramineae	27	*Aster*	6
Salicaceae	15	*Cypripedium*	6
Rosaceae	14	*Solidago*	6
Labiatae	13	*Galium*	5
Orchidaceae	13	*Gentiana*	5
Scrophulariaceae	9	*Juncus*	5
Leguminosae	8	*Viola*	5
Onagraceae	7		

Table 6. Summary of the number of rare vascular plants in the northeastern Iowa fen flora for different rarity classifications.

Source	Number	Percent of Total Flora	Percent of Native Flora
Native species rare on Iowan surface: based on Eilers (1971) and Cooperrider (1962)	97	30%	32%
Rare in Iowa: Howe et al. (1984)	63	20%	21%
Endangered in Iowa: Roosa et al. (1989)	21	7%	7%
Threatened in Iowa: Roosa et al. (1989)	11	3%	4%
Special concern in Iowa: Roosa et al. (1989)	6	2%	2%
New to Iowan surface: based on Eilers (1971) and Cooperrider (1962)	34	11%	11%
New to state	13	4%	4%
Total native rare taxa	134	44%	42%
Total exotic rare taxa	4	1%	

Stability and Distribution of the Vascular Plant Flora

Only seven taxa (*Carex diandra, Cassia marilandica, Eleocharis acicularis, Eriophorum gracile, Filipendula rubra, Salix lucida,* and *Selaginella eclipes*) which had been previously reported from northeastern Iowa fens were not located during the course of this study. Of these taxa, only *Carex diandra* is currently considered extirpated from the state (Howe et al., 1984). *Cassia marilandica, Filipendula rubra,* and *Selaginella eclipes* became extirpated from the northeastern Iowa fen flora through site destruction, while the remaining four have become extirpated through loss of populations on extant sites.

The distributions of most species seem relatively unaffected by the environmental variation described above. A few taxa should be pointed out, however, which do appear to be limited in their distribution by environmental factors. For example, one-half of the stations for *Menyanthes trifoliata* occur in oxbow fen sites, even though such sites represent only 4% of extant fens in the region. Some taxa, including *Angelica atropurpurea, Artemisia serrata, Lobelia kalmii,* and *Triglochin maritimum* are largely restricted to the northwestern portion of the study area where

precipitation tends to be lowest and soil pH, Ca, and Mg tend to be highest. Additional taxa, including *Botrychium multifidum, Botrychium simplex, Carex leptalea, Dryopteris ×uliginosa, Equisetum ×littorale, Eriophorum virginicum, Habenaria flava* var. *herbiola, Ludwigia palustris, Osmunda regalis, Panicum boreale, Rhexia virginica, Solidago patula, Viola lanceolata,* and *Viola primulifolia* are restricted to the south and southeast where they are usually found in low-pH, low-organic matter, low-Mg, and low-Ca eolian sand fens. This part of the study area also has the highest temperature and precipitation.

Rare Taxa in the Northeastern Iowa Fen Flora

A remarkable number of the taxa included in the flora of northeastern Iowa fens are rare in the region and state. Approximately 44% of the flora (138 taxa) fall into one of the five categories of rarity (Tables 6 and 7). Four of these are rare exotic weeds. Of the native taxa, 97 (30% of the flora) are rare in northeastern Iowa, 63 (20%) are rare in the state, 38 (12%) are listed by the Iowa DNR for Iowa Endangered Species Act protection, 34 (11%) are new to northeastern Iowa, and 13 (4%) are new to the state. Approximately 12% of all state rare taxa (Howe et al., 1984), and 17% of all Iowa 'endangered', 'threatened', and 'special concern' species (Roosa et al., 1989) occur in northeastern Iowa fen sites.

While certainly important for rare species, fens also contribute greatly to the total vascular plant biodiversity in the region and state. Even though fen habitats originally occupied approximately only .1% of the northeastern Iowa landscape (and currently cover less than .01% of the land surface), these sites harbor approximately 28% of the total flora of the Iowan Erosional Surface (based on estimates in Eilers, 1971) and 18% of the state's total flora (based on estimates from John Kartesz, pers. comm.).

CONCLUSIONS

Fens in northeastern Iowa represent a diverse collection of habitats which vary in their surficial geology, soils, and climate. These fen sites harbor a substantial proportion of both the total diversity of the Iowa flora and the rare components of that flora.

Of all the results presented above, perhaps none is more im-

Table 7. List of rare Iowa plants found in northeastern Iowa fens.

Taxon	Iowa Rare	New to NE Iowa	New to Iowa	DNR Rank
Alnus rugosa	x			
Angelica atropurpurea	x			SC
Artemesia serrata	x			
Aster junciformis	x			E
Aster puniceus	x			
Betula pumila var. *glandulifera*	x			SC
Betula × *sanbergii*		x	x	
Botrychium multifidum	x	x		E
Botrychium simplex	x			E
Cacalia suaveolens	x			T
Calamagrostis inexpansa		x		
Callitriche heterophylla	x			T
Carex diandra	x			
Carex frankii	x			
Carex granularis		x		
Carex lasiocarpa var. *ammericana*		x		
Carex leptalea	x	x		E
Carex prairea	x			
Carex rostrata var. *utriculata*	x			
Carex sartwellii	x			
Carex sterilis		x	x	
Carex tetanica	x			
Cirsium muticum	x			
Cornus stolonifera	x			
Cypripedium candidum	x			T
Cypripedium parviflorum		x	x	
Cypripedium pubescens	x			
Cypripedium reginae	x			E
Cypripedium × *andrewsii*	x	x		
Cypripedium × *favillianum*		x	x	
Cystopteris fragilis var. *fragilis*		x		
Dryopteris × *uliginosa*		x		
Eleocharis elliptica		x		
Eleocharis smallii		x		
Epilobium strictum		x	x	
Equisetum fluviatile	x			
Equisetum sylvaticum	x			E
Equisetum × *littorale*		x		
Eriophorum angustifolium				SC
Eriophorum gracile	x			E
Eriophorum virginicum		x	x	
Filipendula rubra	x			E
Galium labradoricum	x			E
Galium trifidum	x			
Gentiana crinita	x			

Table 7. Continued.

Taxon	Iowa Rare	New to NE Iowa	New to Iowa	DNR Rank
Gentiana crinita × *procera*		x	x	
Gentiana procera	x			T
Habenaria flava var. *herbiola*	x			E
Habenaria hyperborea	x	x		T
Habenaria praeclara	x			E
Habenaria psycodes	x			T
Hypericum majus	x			
Liatris ligulistylis	x			
Liparis loeselii	x			
Lobelia kalmii	x	x		T
Melanthium virginicum	x			
Menyanthes trifoliata	x			E
Mimulus glabratus var. *fremontii*	x			E
Muhlenbergia glomerata	x			
Ophioglossum vulgatum	x			SC
Osmunda regalis	x			E
Panicum boreale		x		E
Parnassia glauca	x			
Pilea fontana	x			
Rhexia virginica	x			E
Rhynchospora capillacea	x	x		T
Rubus pubescens	x	x		
Rumex orbiculatus	x			
Salix candida	x			SC
Salix lucida	x			E
Salix pedicellaris var. *hypoglauca*	x			T
Salix sericea	x	x		
Salix × *clarkei*		x	x	
Salix × *rubella*		x	x	
Salix × *subsericea*		x		
Salix × *cryptodonta*		x	x	
Salix candida × *pedicellaris*		x	x	
Scleria verticillata	x	x		E
Selaginella eclipes	x			E
Solidago patula	x			E
Solidago uliginosa		x	x	
Spiranthes lucida		x	x	E
Triadenum fraseri	x			
Triglochin maritimum	x	x		T
Triglochin palustre	x	x		T
Valeriana edulis	x			SC
Viola primulifolia	x			

portant than the wholesale destruction of this habitat, which had led to the loss of 93% of sites and of the complex spatial structure once present from township to regional scales. Sites are now more isolated than formerly, leading to an almost certain reduction in the rate of immigration between sites and in the rate (and direction of) migration of fen species across this landscape. It is essential that site isolation not increase further if fen species are to be given optimal chance of migration, as the past history of sites indicates that their habitats may not survive global warming.

Only 14 sites out of the 160 extant (Brayton-Horsley, Cutshall Access, Freeport, Elk Creek, Mark Sand Prairie, Nichols, Northwoods Park, Rowley, Rowley North, Slough Creek 1, Split Rock Park, Spring Creek 2, Wiese Slough, Worth Pond) are currently owned and protected by private or public conservation organizations. The remaining 146 sites are largely under private ownership. While most private landowners of fen sites have expressed interest in protecting their sites, a few are endangering sites. Since initiation of survey work, three sites (Grassley's Folly, Mark Sand South, and Temple Hill) have been badly damaged (and perhaps destroyed) through draining or grazing.

To protect the remaining biodiversity of this habitat, and to provide optimal migration ability for species in the event of climate change, all extant fens in northeastern Iowa must be afforded some form of protection, either through private landowner action or through the purchase of sites when they become endangered. It is essential that conservation organizations in the state make fen protection a priority to ensure that the physical and biological diversity documented here will be protected into the 21st century.

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CURRICULUM IN ECOLOGY
229 WILSON HALL, CB #3275
UNIVERSITY OF NORTH CAROLINA
CHAPEL HILL, NC 27514

APPENDIX I. INVENTORY OF EXTANT NORTHEASTERN IOWA FEN SITES.

Site Name	Size (ha)	Geo-logic class	Site Location
Allamakee County			
Clear Creek 1	1.3	F	NW¼ SE¼ NW¼ Sec. 27, T. 100 N, R. 5 W
Clear Creek 2	0.4	F	SW¼ NE¼ NW¼ Sec. 27, T. 100 N, R. 5 W
Benton County			
Boar Power	0.3	T	SE¼ NE¼ NE¼ Sec. 12, T. 86 N, R. 9 W
Elberon	1.2	T	SE¼ NW¼ Sec. 17, T. 83 N, R. 12 W
Gilchrist	1.8	T	SE¼ NW¼ SE¼ Sec. 12, T. 86 N, R. 9 W
Mt. Auburn	28.8	T	S½ NE¼ Sec. 23, T. 86 N, R. 11 W
Black Hawk County			
Dunkerton SE 1	12.1	T	SE¼ NE¼ NE¼ Sec. 11, T. 89 N, R. 11 W
Dunkerton SE 2	15.5	T	NW¼ SE¼ Sec. 2, T. 89 N, R. 11 W
Hammond Road	1.6	T	NE¼ NW¼ SE¼ Sec. 15, T. 87 N, R. 13 W
Mark Sand North	1.2	E	SW¼ NW¼ Sec. 19, T. 90 N, R. 14 W
Mark Sand South	3.6	E	S½ SE¼ SW¼ Sec. 19, T. 90 N, R. 14 W
St. Francis	0.4	T	NW¼ NW¼ NW¼ Sec. 8, T. 89 N, R. 11 W
St. John	6.3	T	NE¼ NW¼ Sec. 27, T. 90 N, R. 12 W
Bremer County			
Brayton-Horsley	4.7	T	N½ NW¼ SE¼ Sec. 2, T. 92 N, R. 11 W
Bushing	2.0	T	SW¼ NE¼ NW¼ Sec. 36, T. 93 N, R. 14 W
Frederika	0.9	T	NW¼ NE¼ SW¼ Sec. 13, T. 93 N, R. 13 W
Horsley	0.3	T	NW¼ SE¼ SE¼ Sec. 2, T. 92 N, R. 11 W
Northwoods Park	3.4	O	SW¼ NE¼ SE¼ Sec. 13, T. 93 N, R. 11 W
Plainfield	0.3	T	SE¼ NE¼ NE¼ Sec. 31, T. 93 N, R. 14 W
Waverly North	0.6	T	SE¼ NE¼ NE¼ Sec. 14, T. 92 N, R. 14 W
Buchanan County			
Amish	8.8	T	NW¼ NE¼ SW¼ Sec. 18, T, 90 N, R. 9 W
Cutshall Access	4.0	O	NE¼ NE¼ SW¼ Sec. 6, T. 89 N, R. 10 W
Masonville	1.0	T	SE¼ NE¼ NW¼ Sec. 13, T. 89 N, R. 7 W
Otterville	1.5	T	W½ NE¼ NE¼ Sec. 14, T. 89 N, R. 10 W
Rowley	2.2	T	NW¼ SE¼ SE¼ Sec. 2, T. 87 N, R. 9 W
Rowley North	0.1	T	NE¼ NE¼ SE¼ Sec. 2, T. 87 N, R. 9 W
Rowley West	6.7	T	SW¼ SE¼ SE¼ Sec. 5, T. 87 N, R. 9 W

APPENDIX I. Continued.

Site Name	Size (ha)	Geo-logic class	Site Location
Walker Sand Ridge North	0.5	E	SE¼ NW¼ SW¼ Sec. 31, T. 87 N, R. 8 W
Walker Sand Ridge South	0.9	E	SW¼ SW¼ SW¼ Sec. 31, T. 87 N, R. 8 W
Winthrop West	4.0	T	N½ SW¼ NW¼ Sec. 33, T. 89 N, R. 8 W
Butler County			
Allison East 1	1.4	T	SE¼ NE¼ SE¼ Sec. 35, T. 92 N, R. 16 W
Allison East 2	1.0	T	SW¼ NE¼ SE¼ Sec. 35, T. 92 N, R. 16 W
Allison East 3	2.7	T	NW¼ NE¼ SE¼ Sec. 35, T. 92 N, R. 16 W
Allison West	0.7	T	SW¼ NW¼ NE¼ Sec. 27, T. 92 N, R. 17 W
Austinville	0.1	B	SW¼ NW¼ NW¼ Sec. 19, T. 90 N, R. 18 W
Big Rock	1.5	T	NW¼ NE¼ NW¼ Sec. 22, T. 92 N, R. 16 W
Clarksville NE	0.9	T	NW¼ SE¼ NW¼ Sec. 35, T. 93 N, R. 15 W
Clarksville South	0.6	T	SW¼ SW¼ SE¼ Sec. 19, T. 92 N, R. 15 W
Dumont	1.2	T	SE¼ SE¼ SE¼ Sec. 18, T. 92 N, R. 18 W
Ft. Sumpter 1	7.7	T	S½ NW¼ NE¼ Sec. 8, T. 91 N, R. 17 W
Ft. Sumpter 2	0.8	T	SW¼ SW¼ SW¼ Sec. 5, T. 91 N, R. 17 W
Ft. Sumpter 3	7.3	T	SE¼ NW¼ SE¼ Sec. 10, T. 91 N, R. 17 W
New Albion	1.0	T	SE¼ SW¼ SW¼ Sec. 9, T. 90 N, R. 16 W
Pilot Rock	0.7	T	SE¼ SE¼ NE¼ Sec. 21, T. 92 N, R. 17 W
Cedar County			
Rochester South	0.9	E	SW¼ NE¼ SE¼ Sec. 25, T. 79 N, R. 3 W
Cerro Gordo County			
Buffalo Slough	12.6	O	E½ SW¼ NE¼ Sec. 34, T. 97 N, R. 20 W
Fertile	6.1	T	NE¼ NE¼ NW¼ Sec. 6, T. 97 N, R. 21 W
Neuhring	1.0	T	NE¼ NE¼ SW¼ Sec. 15, T. 97 N, R. 21 W
Pope	0.3	T	NE¼ SW¼ NW¼ Sec. 9, T. 97 N, R. 21 W
Rockwell	0.9	B	NW¼ SW¼ SW¼ Sec. 10, T. 94 N, R. 20 W
Wheelerwood	2.3	B	SE¼ SE¼ NE¼ Sec. 15, T. 97 N, R. 21 W
Winnebago 1	0.4	T	SW¼ NE¼ SE¼ Sec. 5, T. 97 N, R. 21 W
Winnebago 2	0.5	T	NW¼ SE¼ SE¼ Sec. 9, T. 97 N, R. 21 W
Chickasaw County			
Alpha East	0.3	T	SE¼ SE¼ SE¼ Sec. 1, T. 94 N, R. 11 W
Barker Station	1.2	T	NE¼ SW¼ SW¼ Sec. 25, T. 94 N, R. 12 W
Boyd	26.3	T	SE¼ NE¼ NE¼ Sec. 33, T. 95 N, R. 12 W
Boyd North	0.3	T	NW¼ SE¼ SE¼ Sec. 21, T. 95 N, R. 12 W
Boyd South	3.4	T	NE¼ NE¼ SW¼ Sec. 34, T. 95 N, R. 12 W
Bradford North	1.5	T	SE¼ SE¼ SE¼ Sec. 4, T. 94 N, R. 14 W
Chickasaw 1	18.4	T	SW¼ NW¼ SW¼ Sec. 28, T. 95 N, R. 14 W
Chickasaw 2	3.5	T	SE¼ NE¼ NW¼ Sec. 28, T. 95 N, R. 14 W
East Fork	3.1	T	NE¼ NW¼ SW¼ Sec. 5, T. 95 N, R. 12 W

APPENDIX I. Continued.

Site Name	Size (ha)	Geo-logic class	Site Location
Grassley's Folly	13.0	T	SW¼ SW¼ SW¼ Sec. 13, T. 95 N, R. 12 W
Kleiss	1.6	T	SW¼ SE¼ NE¼ Sec. 26, T. 95 N, R. 11 W
Lawler East	4.9	T	NE¼ NW¼ NW¼ Sec. 11, T. 95 N, R. 11 W
Lawler NW	20.3	T	SW¼ SW¼ SW¼ Sec. 32, T. 96 N, R. 11 W
Lawler SE	6.5	T	NW¼ NE¼ NE¼ Sec. 22, T. 95 N, R. 11 W
Marsh Creek	1.1	T	NE¼ NE¼ NW¼ Sec. 21, T. 94 N, R. 11 W
New Hampton East	36.7	T	S½ SE¼ SW¼ Sec. 8, T. 95 N, R. 12 W
New Hampton North	2.2	T	NW¼ SW¼ SE¼ Sec. 32, T. 96 N, R. 12 W
Simpson Creek 1	3.7	T	NE¼ SW¼ SE¼ Sec. 21, T. 95 N, R. 11 W
Simpson Creek 2	5.5	T	SW¼ NE¼ NE¼ Sec. 28, T. 95 N, R. 11 W
Simpson Creek 3	2.3	T	NE¼ NE¼ SW¼ Sec. 27, T. 95 N, R. 11 W
Split Rock	1.0	T	SW¼ SW¼ SW¼ Sec. 35, T. 94 N, R. 12 W
Stapleton Church	0.8	T	NW¼ SE¼ SE¼ Sec. 23, T. 95 N, R. 11 W
Two Mile Creek	1.8	T	SW¼ SW¼ SE¼ Sec. 36, T. 95 N, R. 14 W
Clayton County			
Postville	37.5	T	NW¼ Sec. 21, T. 95 N, R. 6 W
Strawberry Point	9.7	T	SW¼ NE¼ NW¼ Sec. 25, T. 91 N, R. 6 W
Clinton County			
Mockridge	0.2	E	SE¼ NW¼ NE¼ Sec. 36, T. 82 N, R. 1 E
Springeponde	8.3	T	NE¼ NW¼ SW¼ Sec. 23, T. 81 N, R. 2 E
Toronto 1	0.1	E	SE¼ SW¼ NW¼ Sec. 24, T. 82 N, R. 1 E
Toronto 2	1.3	E	NE¼ SE¼ NE¼ Sec. 23, T. 82 N, R. 1 E
Delaware County			
Hawker	7.3	T	NW¼ NE¼ NW¼ Sec. 22, T. 89 N, R. 6 W
Robinson	9.9	T	SE¼ NW¼ SW¼ Sec. 19, T. 87 N, R. 6 W
Dubuque County			
Epworth	0.2	B	SW¼ NE¼ SE¼ Sec. 4, T. 88 N, R. 1 W
Farley	0.2	B	NE¼ NW¼ NW¼ Sec. 4, T. 88 N, R. 1 W
Fayette County			
Alpha NW	2.7	T	NW¼ SE¼ NW¼ Sec. 29, T. 95 N, R. 10 W
Alpha SE 1	0.1	T	SW¼ SE¼ SE¼ Sec. 9, T. 94 N, R. 10 W
Alpha SE 2	6.1	T	NE¼ SE¼ SW¼ Sec. 9, T. 94 N, R. 10 W
Hawkeye	26.9	T	SW¼ SE¼ SW¼ Sec. 11, T. 94 N, R. 10 W
Hunter Creek	0.9	T	NE¼ SW¼ SE¼ Sec. 30, T. 91 N, R. 9 W
Oelwein West	4.3	T	E½ NE¼ SE¼ Sec. 13, T. 91 N, R. 10 W
Otter Creek	2.0	T	NW¼ NW¼ NW¼ Sec. 31, T. 92 N, R. 9W
Smithfield Township Hall	3.5	T	SW¼ SE¼ NE¼ Sec. 16, T. 92 N, R. 8 W

APPENDIX I. Continued.

Site Name	Size (ha)	Geo-logic class	Site Location
St. Lucas	2.4	B	S½ SW¼ SW¼ Sec. 4, T. 95 N, R. 9 W
Sumner SE 1	6.4	T	NE¼ SE¼ SE¼ Sec. 6, T. 92 N, R. 10 W
Sumner SE 2	2.6	T	NE¼ SW¼ SE¼ Sec. 6, T. 92 N, R. 10 W
Sumner SE 3	0.6	T	SW¼ SE¼ NW¼ Sec. 32, T. 93 N, R. 10 W
Turner Creek 1	2.1	T	N½ NW¼ SE¼ Sec. 11, T. 94 N, R. 9W
Turner Creek 3	0.2	T	NE¼ NE¼ SE¼ Sec. 11, T. 94 N, R. 9 W
Wadena NW	0.8	B	NW¼ SE¼ SE¼ Sec. 18, T. 93 N, R. 7 W
West Union South	7.1	T	SW¼ NE¼ SW¼ Sec. 5, T. 93 N, R. 8 W
Floyd County			
Charles City East	10.0	T	NE¼ SW¼ SW¼ Sec. 36, T. 96 N, R. 15 W
Charles City West	0.5	T	NW¼ NE¼ SE¼ Sec. 34, T. 96 N, R. 16 W
Rockford	2.3	O	NE¼ NE¼ SW¼ Sec. 10, T. 95 N, R. 18 W
Slough Creek 1	9.3	T	NE¼ SW¼ NE¼ Sec. 21, T. 97 N, R. 16 W
Slough Creek 2	0.8	T	NE¼ NE¼ NE¼ Sec. 22, T. 97 N, R. 16 W
Slough Creek 3	1.0	T	SE¼ NE¼ NE¼ Sec. 22, T. 97 N, R 16 W
Slough Creek 4	1.2	T	NW¼ SE¼ NE¼ Sec. 22, T. 97 N, R. 16 W
Slough Creek 5	4.9	T	NW¼ NE¼ NW¼ Sec. 26, T. 97 N, R. 16 W
Franklin County			
Maynes Creek	1.0	B	NW¼ NE¼ SE¼ Sec. 12, T. 91 N, R. 19 W
Spring Creek 1	11.9	F	NE¼ NW¼ SE¼ Sec. 26, T. 92 N, R. 21 W
Spring Creek 2	0.8	F	SE¼ NE¼ SE¼ Sec. 24, T. 92 N, R. 21 W
Spring Creek 3	1.3	F	NW¼ SE¼ SW¼ Sec. 24, T. 92 N, R. 21 W
Grundy County			
Morrison	1.6	T	N½ SE¼ NW¼ Sec. 15, T. 87 N, R. 16 W
New Hartford	1.4	T	NE¼ NW¼ NE¼ Sec. 5, T. 89 N, R. 15 W
Stout	0.6	T	SW¼ NW¼ NE¼ Sec. 18, T. 89 N, R. 15 W
Wellsburg	4.1	T	NW¼ NW¼ SE¼ Sec. 12, T. 88 N, R. 18 W
Howard County			
Lime Springs	1.8	T	SW¼ SE¼ NE¼ Sec. 27, T. 100 N, R. 12 W
Riceville North	1.2	T	SW¼ SW¼ SW¼ Sec. 8, T. 99 N, R. 14 W
Schley	21.5	T	W½ SW¼ NW¼ Sec. 16, T. 98 N, R. 11 W
Staff Creek	2.4	T	NW¼ SE¼ SW¼ Sec. 28, T. 100 N, R. 14 W
Turkey River	8.5	T	NW¼ NE¼ SW¼ Sec. 31, T. 98 N, R. 11 W
Johnson County			
Coralville	0.2	T	SE¼ NE¼ SE¼ Sec. 20, T. 80 N, R. 6 W
Jones County			
Olin	2.1	E	NW¼ SW¼ SE¼ Sec. 6, T. 83 N, R. 2 W
Temple Hill	0.3	E	NE¼ NW¼ NE¼ Sec. 17, T. 85 N, R. 1 W

APPENDIX I. Continued.

Site Name	Size (ha)	Geologic class	Site Location
Walnut Creek 1	0.8	T	NE¼ NE¼ SE¼ Sec. 32, T. 84 N, R. 4 W
Walnut Creek 2	1.1	T	SE¼ NW¼ SW¼ Sec. 33, T. 84, N, R. 4 W
White Oak Creek	1.0	T	NE¼ SE¼ NE¼ Sec. 26, T. 83 N, R. 4 W
Linn County			
Central City	0.3	T	NE¼ NW¼ NE¼ Sec. 9, T. 85 N, R. 6 W
Loupee	15.9	T	E½ NE¼ NE¼ Sec. 14, T. 83 N, R. 6 W
Matus	18.5	T	SE¼ NE¼ Sec. 36, T. 85 N, R. 6 W
Moses Road	0.2	T	NW¼ SE¼ SE¼ Sec. 6, T. 86 N, R. 8 W
Paris	1.1	E	SE¼ NW¼ SW¼ Sec. 30, T. 86 N, R. 6 W
Patton	0.8	T	E½ NW¼ NE¼ Sec. 6, T. 86 N, R. 6 W
Western College	0.6	T	SE¼ NE¼ SE¼ Sec. 35, T. 82 N, R. 7 W
Whittier	1.6	T	NE¼ SW¼ NW¼ Sec. 8, T. 84 N, R. 5 W
Windy Oaks North	0.4	E	SW¼ SE¼ NE¼ Sec. 29, T. 85 N, R. 5 W
Windy Oaks South	0.6	E	NW¼ SW¼ NE¼ Sec. 29, T. 85 N, R. 5 W
Mitchell County			
Little Cedar	0.7	T	SW¼ SE¼ SE¼ Sec. 9, T. 99 N, R. 16 W
McIntire	0.5	T	SE¼ SE¼ SE¼ Sec. 35, T. 100 N, R. 15 W
Osage West	12.4	T	NE¼ NW¼ NE¼ Sec. 34, T. 98 N, R. 18 W
Mona	1.4	T	SW¼ SE¼ SW¼ Sec. 14, T. 100 N, R. 18 W
Riceville NW	2.1	T	SW¼ SE¼ Sec. 15, T. 99 N, R. 15 W
St. Ansgar	2.0	B	NW¼ SW¼ SW¼ Sec. 13, T. 99 N, R. 18 W
Stacyville North	2.4	T	NW¼ SW¼ SE¼ Sec. 30, T. 100 N, R. 16 W
Stacyville SE	0.5	T	N½ SE¼ NW¼ Sec. 9, T. 99 N, R. 16 W
Stone School	1.1	T	NW¼ SE¼ NE¼ Sec. 20, T. 99 N, R. 15 W
Muscatine County			
Conesville	3.0	F	SE¼ NE¼ NE¼ Sec. 20, T. 76 N, R. 4 W
Nichols	49.3	O	NW¼ SE¼ Sec. 23, T. 77 N, R. 4 W
Wiese Slough	19.9	O	E½ SE¼ NE¼ Sec. 13, T. 78 N, R. 3 W
Tama County			
Sand Hill	0.4	E	NE¼ NW¼ SE¼ Sec. 2, T. 82 N, R. 15 W
Winneshiek County			
Dry Run	3.9	B	SE¼ NE¼ SW¼ Sec. 35, T. 98 N, R. 9 W
Freeport	1.4	B	NE¼ NE¼ NE¼ Sec. 14, T. 98 N, R. 8 W
Jackson Junction	1.4	T	NE¼ SW¼ NE¼ Sec. 20, T. 96 N, R. 10 W
Kendallville South	5.1	T	NW¼ SW¼ SE¼ Sec. 9, T. 99 N, R. 10 W
Madison Church 1	2.8	B	SW¼ NE¼ NE¼ Sec. 16, T. 98 N, R. 9 W

APPENDIX I. Continued.

Site Name	Size (ha)	Geo-logic class	Site Location
Madison			
Church 2	4.6	B	SE¼ NW¼ NE¼ Sec. 21, T. 98 N, R. 9 W
Worth County			
Elk Creek	2.1	F	SW¼ SE¼ NW¼ Sec. 18, T. 99 N, R. 21 W
Worth Pond	50.1	F	SW¼ NE¼ NW¼ Sec. 26, T. 99 N, R. 20 W

Legend for geologic classes: T = pre-Illinoian till site, B = Bedrock site, E = Eolian sand site; F = Fluvial sand site, O = Oxbow site.

APPENDIX II: ANNOTATED CATALOGUE OF VASCULAR PLANT SPECIES FROM NORTHEASTERN IOWA FENS

This annotated catalogue is based on collections and observations made from 1984 to 1991 by J. C. Nekola, and from a survey of the northeastern Iowa botanical literature as detailed under Methods. The nomenclature follows that of Swink and Wilhelm (1979). Where names differ from those of Kartesz (1993), the Kartesz synonym follows in brackets. Following each binomial is a common name, rarity in the northeastern Iowa and entire Iowa flora [using the following abbreviations:

R = Rare in Iowan Erosional surface (Cooperrider, 1962; Eilers, 1971);
L = Listed as rare Iowa plant by Howe et al. (1984);
E = Listed as Endangered by Roosa et al. (1989);
T = Listed as Threatened by Roosa et al. (1989);
SC = Listed as Special Concern by Roosa et al. (1989);
NI = New to Iowan Surface flora (Cooperrider, 1962; Eilers, 1971);
NS = New to state flora]

Taxa incidental in the fen flora are also noted, as is an approximation of the distribution and frequency of each taxa across this region. For selected rare taxa, the number of sites of occurrence is recorded. All exotic taxa are preceded by an '*'.

PTERIDOPHYTES

Equisetaceae

Equisetum arvense L. (Field Horsetail): Incidental. Infrequent throughout on margins.

Equisetum fluviatile L. (Water Horsetail): R, L Scattered throughout. (14 sites)

Equisetum sylvaticum L. (Wood Horsetail): R, L, E Incidental. Rare in extreme north on margins. (1 site)

Equisetum ×*littorale* Kuhlewein ex Rupr.: Rare in extreme east on an eolian sand fen. (1 site)

Ophioglossaceae

Botrychium multifidum (Gmel.) Trev. (Leathery Grape Fern): NI, L, E Incidental. Rare on sandy margins in south central. (2 sites)
Botrychium simplex E. Hitchc. (Small Grape Fern): R, L, E Incidental. Rare on a sandy margin in the south central. (1 site)
Ophioglossum vulgatum L. [*O. pusillim* Raf.] (Adder's Tongue Fern): R, L, SC Scattered in central. (13 sites)

Osmundaceae

Osmunda regalis L. var. *spectabilis* (Willd.) Gray (Royal Fern): R, L, E Incidental. Rare in southeast on moist margins of eolian sand and oxbow fens. (3 sites)

Polypodiaceae
(including *Dryopteraceae, Thelypteraceae*)

Athyrium filix-femina (L.) Roth (Lady Fern): Frequent in east-central.
Cystopteris fragilis (L.) Bernh. var. *fragilis* (Fragile Fern): NI Rare in north. (1 site)
Dryopteris cristata (L.) Gray (Crested Shield Fern): R Frequent in eastern half. (26 sites)
Dryopteris ×*uliginosa* (A. Braun ex Dowell) Druce: NI Rare on a margin in the extreme south. (1 site)
Onoclea sensibilis L. (Sensitive Fern): Abundant and dominant throughout.
Thelypteris palustris Schott (Marsh Fern): Abundant and dominant throughout.

Selaginellaceae

Selaginella eclipes Buck (Northern Marsh Spike Moss): R, L, E Reported (and apparently extirpated) from a single site in Muscatine County (Guldner, 1960). Although known from a calcareous depression in Worth County (Nekola, 1991), no extant fen populations have been observed.

GYMNOSPERMS

Cupressaceae

Juniperus virginiana L. (Red Cedar): Incidental. Uncommon throughout on dry hummocks and margins.

DICOTYLEDONS

Aceraceae

Acer negundo L. (Box Elder): Incidental. Uncommon throughout in thickets and on margins.
Acer saccharinum L. (Silver Maple): Incidental. Rare on margins.

Anacardiaceae

Rhus radicans L. [*Toxicodendron radicans* (L.) Kuntze] (Poison Ivy): Incidental. Rare on margins.

Apocynaceae

Apocynum sibiricum Jacq. [*A. cannabinum* L.] (Indian Dogbane): Incidental. Uncommon throughout.

Asclepiadaceae

Asclepias incarnata L. (Swamp Milkweed): Common throughout.
Asclepias syriaca L. (Common Milkweed): Incidental. Scattered throughout on margins.

Balsaminaceae

Impatiens capensis Meerb. (Spotted Jewelweed): Common throughout in discharge zones.
Impatiens pallida Nutt. (Pale Jewelweed): Rare in discharge zones.

Betulaceae

Alnus rugosa (Regel) Fern. [*Alnus incana* (L.) Moench ssp. *rugosa* (DuRoi) Clausen] (Speckled Alder): L Uncommon in north central, where it is locally dominant. (5 sites)
Betula pumila L. var. *glandulifera* Regel (Bog Birch): R, L, SC Locally common in north central. (20 sites)
Betula ×*sandbergii* Britt. (Sandberg's Birch): NI, NS Rare in north central. (1 site)

Callitrichaceae

Callitriche heterophylla Pursh (Large Water Starwort): R,L,T Incidental. Rare in cold water of discharge streams. (2 sites)

Campanulaceae

Campanula aparinoides Pursh (Marsh Bellflower): Abundant throughout.
Lobelia kalmii L. (Kalm's Lobelia): NI, L, T Rare in northwest on low vegetation mats. (4 sites)
Lobelia siphilitica L. (Great Blue Lobelia): Frequent throughout.

Caprifoliaceae

Sambucus canadensis L. (Elderberry): Infrequent throughout in thickets.
Viburnum lentago L. (Nannyberry): Infrequent throughout in thickets.

Caryophyllaceae

Arenaria lateriflora L. [*Moehringia lateriflora* (L.) Fenzl.] (Wood Sandwort): Incidental. Uncommon in eastern counties.

**Cerastium vulgatum* L. [*Cerastium fontanum* Baumg. ssp. *vulgare* (Hartman) Greuter & Burdet] (Mouse-eared Chickweed): Incidental. Throughout on heavily grazed margins.

Silene nivea (Nutt.) Muhl. ex Otth. (Snowy Campion): R Scattered in southern third.

Stellaria longifolia Muhl. ex Willd. (Stitchwort): Frequent in eastern half.

Compositae

Achillea millefolium L. (Yarrow): Dry hummocks and margins throughout.

Ambrosia artemisiifolia L. (Common Ragweed): Incidental. Rare on dry hummocks.

Ambrosia trifida L. (Giant Ragweed): Locally dominant throughout on disturbed soil.

Artemisia serrata Nutt. (Saw-toothed Sage): L Uncommon on margins in northwest. (5 sites)

Aster ericoides L. (Heath Aster): Incidental. Throughout on dry hummocks.

Aster junciformis Rydb. [*A. borealis* (Torr. & Gray) Prov.] (Rush Aster): R, L, E Rare in north third on cold, wet soil. (4 sites)

Aster novae-angliae L. (New England Aster): Frequent throughout.

Aster praealtus Poir. (Willow Aster): Scattered in east half.

Aster puniceus L. (Swamp Aster): L Abundant throughout. (152 sites)

Aster umbellatus P. Mill. (Flat-top Aster): Common throughout. Most material is referable to the doubtfully distinct *Aster pubentior* Cronq.

Bidens cernua L. (Nodding Bur Marigold): Uncommon throughout on exposed peat.

Bidens coronata (L.) Britt. R (Tall Swamp Marigold): Frequent throughout.

Bidens frondosa L. (Common Beggar's Ticks): Uncommon on disturbed soils.

Boltonia asteroides (L.) L'Her. (False Aster): Common throughout.

Cacalia suaveolens L. [*Synosma suaveolens* (L.) Raf. ex Britt.] (Sweet Indian Plantain): R, L, T Scattered and rare on margins and shrub thickets. (2 sites)

Cirsium altissimum (L.) Hill (Tall Thistle): R Incidental. Scattered on disturbed soils.

**Cirsium arvense* (L.) Scop. (Canadian Thistle): Incidental. Infrequent on disturbed margins.

Cirsium discolor (Muhl. ex Willd.) Spreng. (Pasture Thistle): Incidental. Infrequent on margins.

Cirsium muticum Michx. (Swamp Thistle): R, L Common in northwest, rare and scattered elsewhere. (30 sites)

Erechtities hieraciifolia (L.) Raf. ex DC. (Fireweed): R Scattered throughout on exposed peat.

Eupatorium maculatum L. (Spotted Joe-pye Weed): Common throughout.

Eupatorium perfoliatum L. (Common Boneset): Frequent throughout on mineral-rich soil.

Eupatorium rugosum Houtt. [*Ageratina altissima* (L.) King & H. E. Robins. var. *altissima*] (White Snakeroot): Incidental. Rare in south.
Helenium autumnale L. (Sneezeweed): Common throughout. One of the most conspicuous late-summer flowering plants.
Helianthus grosserratus Martens (Sawtooth Sunflower): Common throughout, becoming most abundant on disturbed areas.
Lactuca canadensis L. (Wild Lettuce): Incidental. Infrequent on margins.
Liatris ligulistylis (Nels.) Schum. (Northern Blazingstar): R, L Incidental. Rare in northwest on margins.
Liatris pycnostachya Michx. (Prairie Blazingstar): Uncommon in north half.
Rudbeckia hirta L. (Black-eyed Susan): Abundant throughout.
Senecio aureus L. (Golden Ragwort): R Frequent locally in northern half.
Senecio pauperculus Michx. (Common Ragwort): Incidental. Rare on dry hummocks on margins.
Silphium perfoliatum L. (Cup Plant): Incidental. Rare on margins.
Solidago altissima L. [*S. canadensis* L.] (Tall Goldenrod): Abundant throughout. Increases in dominance with disturbance.
Solidago gigantea Ait. (Late Goldenrod): Scattered throughout north half.
Solidago graminifolia (L.) Salisb. [*Euthamia graminifolia* (L.) Nutt.] (Grass-leaved Goldenrod): Common throughout.
Solidago patula Muhl. ex Willd. R, L, E (Broad-leaved Goldenrod): Rare in extreme south. (1 site)
Solidago riddellii Frank ex Riddell (Riddell's Goldenrod): R Frequent throughout, but less common in southeast. (62 sites)
Solidago uliginosa Nutt. (Bog Goldenrod): NI, NS Rare in northeast. (2 sites)
**Sonchus asper* (L.) Hill. (Sow Thistle): R Rare on disturbed areas throughout.
**Taraxacum officinale* Weber (Common Dandelion): Frequent throughout. This is the most frequently encountered exotic species.
Vernonia fasciculata Michx. (Common Ironweed): Frequent throughout on margins.

Convolvulaceae
(including *Cuscutaceae*)

Convolvulus sepium L. [*Calystegia sepium* (L.) R. Br.] (Hedge Bindweed): Incidental. Rare on margins.
Cuscuta cephalanthi Engelm. (Buttonbush Dodder): R Infrequent on tall herbaceous plants.

Cornaceae

Cornus alternifolia L. f. (Alternate-leaved Dogwood): Incidental. Rare in thickets.
Cornus obliqua Raf. [*C. amomum* P. Mill. ssp. *obliqua* (Raf.) J. S. Wilson] (Pale Dogwood): Frequent throughout in thickets.
Cornus stolonifera Michx. [*C. sericea* L. ssp. *sericea*] (Red-osier Dogwood): R, L Scattered throughout, but most common in north half in thickets.

Cruciferae

Cardamine bulbosa (Schreb. ex Muhl.) BSP (Bulbous Cress): Abundant throughout.
**Nasturtium officinale* R. Br. [*Rorippa nasturtium-aquaticum* (L.) Hayek] (Water Cress): R Scattered throughout in cold, flowing water of discharge streams.

Cucurbitaceae

Echinocystis lobata (Michx.) T. & G. (Wild Cucumber): Incidental. Rare vine of thickets.

Euphorbiaceae

Acalypha rhomboidea Raf. [*A. virginica* L. var. *rhomboidea* (Raf.) Cooperrider] (Three-seeded Mercury): Frequent throughout on dry hummocks.

Gentianaceae

Gentiana andrewsii Griseb. (Bottle Gentian): Common throughout.
Gentiana crinita Froel. [*Gentianopsis crinita* (Froel) Ma] (Large Fringed Gentian): R, L Locally common in south half. (34 sites)
Gentiana procera Holm [*Gentianopsis procera* (Holm) Ma] (Small Fringed Gentian): R, L, T Locally common in north half. (21 sites)
Gentiana quinquefolia L. [*Gentianella quinquefolia* (L.) Sm.] (Stiff Gentian): Scattered throughout.
Gentiana crinita Froel. × *Gentiana procera* Holm: NI, NS Rare in north central. (1 site)

Hypericaceae

Hypericum majus (Gray) Britt. (Small St. John's Wort): L Scattered throughout on hummocks and disturbed soil.
Hypericum punctatum Lam. (Spotted St. John's Wort): Incidental. Rare in margins.
Hypericum pyramidatum Ait. [*Hypericum ascyron* L.] (Great St. John's Wort): Frequent in east half.
Hypericum sphaerocarpum Michx. (Round-fruited St. John's Wort): Scattered throughout.
Triadenum fraseri (Spach) Gl. (Marsh St. John's Wort): R, L Locally common except in northwest. (54 sites)

Labiatae

Lycopus americanus Muhl. ex W. Bart. (Common Water Horehound): Abundant throughout.
Lycopus uniflorus Michx. (Northern Bugleweed): Less common, but found throughout.
Lycopus virginicus L. (Bugleweed): R Scattered throughout.

Mentha arvensis L. (Wild Mint): Scattered throughout.
Monarda fistulosa L. (Wild Bergamot): Incidental. Frequent on margins.
Physostegia virginiana (L.) Benth. (Obedient Plant): Scattered throughout.
**Prunella vulgaris* L. (Self Heal): Incidental. Throughout on margins, dry hummocks and disturbed, dry soil.
Pycnanthemum virginianum (L.) Durant & Jackson ex B. L. Robins & Fern. (Common Mountain Mint): Abundant throughout.
Scutellaria galericulata L. (Marsh Skullcap): R Frequent in south half, scattered elsewhere. (33 sites)
Scutellaria lateriflora L. (Mad-dog Skullcap): Uncommon on margins.
Stachys palustris L. (Woundwort): Frequent.
Stachys tenuifolia Willd. (Smooth Hedge Nettle): Occasional in south half.
Teucrium canadense L. (Wild Germander): Rare in east central.

Leguminosae

Amorpha fruticosa L. (Indigo Bush): Occasional in east half in shrub thickets.
Amphicarpa bracteata (L.) Fern. (Hog Peanut): Incidental. Rare on margins.
Apios americana Medik. (Ground Nut): R Incidental. Rare on margins.
Cassia marylandica L. [*Senna marilandica* (L.) Link] (Wild Senna): R Incidental? Reported from a single, destroyed Muscatine County site (Guldner, 1960).
Desmodium canadense (L.) DC. (Showy Tick Trefoil): Incidental. Scattered on dry hummocks and margins.
Lathyrus palustris L. (Marsh Vetchling): Common throughout.
Lathyrus venosus Muhl. ex Willd. (Veiny Pea): Incidental. Rare on dry margins.
Strophostyles helvula (L.) Ell. (Trailing Wild Bean): Incidental. Rare on dry margins.

Lythraceae

Lythrum alatum Pursh (Winged Loosestrife): Abundant throughout. Often reaches highest dominance in zones of low vegetation.

Melastomataceae

Rhexia virginica L. (Meadow Beauty): R, L, E Incidental. Rare on an eastern eolian sand site, in proximity to a vernal pool. (1 site)

Menyanthaceae

Menyanthes trifoliata L. (Buckbean): R, L, E Uncommon throughout, preferring very wet soil. (6 sites)

Oleaceae

Fraxinus nigra Marsh. (Black Ash): Incidental. Occasional in shrub thickets and dry margins.

Onagraceae

Epilobium coloratum Biehler (Cinnamon Willow Herb): Frequent throughout.
Epilobium glandulosum Lehm. [*E. ciliatum* Raf. ssp. *glandulosum* (Lehm.) Hoch & Raven] (Northern Willow Herb): R Scattered throughout. Often difficult to separate from the preceding taxa.
Epilobium leptophyllum Raf. (Fen Willow Herb): R Frequent throughout. (58 sites)
Epilobium strictum Muhl. ex Spreng. (Downy Willow Herb): NI, NS Rare in central. (5 sites)
Ludwigia palustris (L.) Ell. (Marsh Purslane): R Incidental. Rare on wet sand of discharge streams in east.
Oenothera biennis L. (Common Evening Primrose): Incidental. Rare on dry hummocks and margins.
Oenothera pilosella Raf. (Prairie Sundrops): Rare in extreme south.

Oxalidaceae

Oxalis violacea L. (Violet Wood Sorrel): Incidental. Rare on margins.

Polemoniaceae

Phlox maculata L. (Wild Sweet William): Common throughout.
Phlox pilosa L. (Prairie Phlox): Incidental. Occasional on dry hummocks and margins in west half.
Polemonium reptans L. (Jacob's Ladder): Frequent in east half.

Polygonaceae

Polygonum amphibium L. (Water Knotweed): R Scattered in east half.
Polygonum pensylvanicum L. (Pennsylvania Knotweed): Common throughout.
Polygonum sagittatum L. (Arrow-leaved Tear-thumb): Abundant throughout, becoming dominant with disturbance.
Rumex orbiculatus Gray (Great Water Dock): R, L Frequent throughout in very wet soils.

Primulaceae

Dodecatheon meadia L. (Shooting Star): Incidental. Rare in east central on dry margins.
Lysimachia ciliata L. (Fringed Loosestrife): Incidental. Scattered in central.
Lysimachia quadriflora Sims (Narrow-leaved Loosestrife): Abundant throughout, becoming most dominant in low vegetation mats.
Lysimachia terrestris (L.) BSP. (Swamp Candles): Incidental. Rare in margins.
Lysimachia thyrsiflora L. (Tufted Loosestrife): R Scattered throughout, often in very wet soil. (13 sites)

Ranunculaceae

Anemone canadensis L. (Canada Anemone): Incidental. Frequent on margins.
Anemone quinquefolia L. (Wood Anemone): Incidental. Rare on dry hummocks.
Caltha palustris L. (Marsh Marigold): Abundant throughout.
Ranunculus pensylvanicus L. f. (Bristly Buttercup): Frequent in east half.
Thalictrum dasycarpum Fisch. & Lall. (Common Meadow Rue): Common throughout.

Rosaceae

Agrimonia parviflora Ait. (Swamp Agrimony): R Frequent throughout.
Filipendula rubra (Hill) B. L. Robins. (Queen of the Prairie): R, L, E No extant populations seen on fen habitats although an old report exists from a Muscatine County site.
Fragaria virginica Duchesne (Wild Strawberry): Common throughout on dry hummocks and margins.
Geum aleppicum Jacq. (Yellow Avens): R Frequent throughout. More common than following species.
Geum laciniatum Murr. (Rough Avens): Occasional in dry margins.
Potentilla norvegica L. (Rough Cinquefoil): Frequent in disturbed sites.
Potentilla palustris (L.) Scop. [*Comarum palustre* L.] (Marsh Cinquefoil): R Rare throughout, absent from southeast. Prefers very wet soils. (7 sites)
Potentilla simplex Michx. (Common Cinquefoil): Incidental. Occasional on margins and dry hummocks.
Prunus virginica L. (Choke Cherry): Incidental. Rare in margins and thickets.
Rosa blanda Ait. (Early Wild Rose): Scattered throughout.
Rosa carolina L. (Pasture Rose): More common than preceding on dry hummocks and margins throughout.
Rubus occidentalis L. (Black Raspberry): Incidental. Rare in shrub thickets and margins.
Rubus pubescens Raf. (Dwarf Raspberry): NI, L Scattered and rare throughout. (8 sites)
Spiraea alba DuRoi (Meadowsweet): Common throughout.

Rubiaceae

Galium boreale L. (Northern Bedstraw): Frequent in east half on dry hummocks and margins.
Galium labradoricum (Wieg.) Wieg. (Bog Bedstraw): R, L, E Rare in north half. (4 sites)
Galium obtusum Bigelow (Wild Madder): Common throughout.
Galium tinctorium (L.) Scop. (Stiff Bedstraw): Occasional throughout.
Galium trifidum L. (Small Bedstraw): R, L Rare in north half in very wet soil. (2 sites)

Salicaceae

Populus tremuloides Michx. (Trembling Aspen): Occasional in northeast in thickets and margins.
Salix bebbiana Sarg. (Beaked Willow): Common in north half.
Salix candida Fluegge ex Willd. (Sage Willow): R, L, SC Locally frequent except in extreme east, where absent. (50 sites)
Salix discolor Muhl. (Pussy Willow): Common throughout.
Salix interior Rowlee. [*S. exigua* Nutt.] (Sandbar Willow): Incidental. Scattered on margins and discharge streams.
Salix lucida Muhl. (Shining Willow): R, L, E Rare in north half. No extant populations observed, but historical collections exist from at least three of the sites inventoried (Fitzpatrick, 1899; Tolstead, 1938; Hartley, 1966; Eilers, 1971).
Salix pedicellaris Pursh (Bog Willow): R, L, T Scattered and rare in north half. (11 sites)
Salix petiolaris Sm. (Petioled Willow): Common throughout.
Salix rigida Muhl. [*S. eriocephala* Michx.] (Heart-leaved Willow): Common throughout.
Salix sericea Marsh. (Silky Willow): NI, L Scattered in central. (5 sites)
Salix ×*clarkei* Bebb. (Clark's Willow): NI, NS Scattered over range of *S. candida.* (23 sites)
Salix ×*cryptodonta* Fern.: NI, NS Rare in west central. (2 sites)
Salix ×*rubella* Bebb. (Red Willow): NI, NS Scattered over range of *S. candida,* but less frequent than preceding. (13 sites)
Salix ×*subsericea* (Anders.) Schn. [*S. petiolaris* Sm.]: NI A few perplexing intermediates between *S. petiolaris* and *S. sericea* have been located in the north half, and may represent this taxon.
Salix candida Fluegge × *Salix pedicellaris* Pursh: NI, NS Very rare in sites of parental co-occurrence. (2 sites)

Santalaceae

Comandra richardsiana Fern. [*Comandra umbellata* Nutt. var. *umbellata*] (Bastard Toadflax): Incidental. On dry hummocks and margins.

Saxifragaceae
(including *Grossulariaceae*)

Heuchera richardsonii R. Br. (Prairie Alum Root): Incidental. Scattered throughout on dry hummocks and margins.
Parnassia glauca Raf. (Grass-of-Parnassis): R, L Frequently scattered throughout. (39 sites)
Penthorum sedoides L. (Ditch Stonecrop): Incidental. Occasional on muddy, disturbed margins.
Ribes americanum P. Mill. (Wild Black Currant): Scattered in north half in shrub thickets.
Saxifraga pensylvanica L. (Swamp Saxifrage): Common in all but northwest.

Scrophulariaceae

Chelone glabra L. (Turtlehead): R Common throughout. Six sites support populations of the fen restricted butterfly *Euphydryas phaeton phaeton*, which obligately feeds on this species.

Agalinis paupercula (Gray) Britt. (Fen False Foxglove): Scattered in central. Populations growing in very wet, cold soil approach var. *borealis* Pennell. (16 sites)

Agalinis purpurea (L.) Pennell (Purple False Foxglove): Scattered in southeast third. It is perhaps best to lump this and the preceding species, although *G. paupercula* var. *borealis* is quite distinct.

Agalinis tenuifolia (Vahl) Raf. (Slender False Foxglove): Incidental. Rare in extreme south.

Gratolia neglecta Torr. (Clammy Hedge Hyssop): Incidental. Rare in south third on muddy margins.

Mimulus glabratus HBK var. *fremontii* (Benth.) Grant. [*M. g.* var. *jamesii* (Torr. & Gray ex Benth.) Gray] (Yellow Monkeyflower): R, L, E Rare in discharge streams. (3 sites)

Mimulus ringens L. (Monkeyflower): Common throughout on margins.

Pedicularis lanceolata Michx. (Fen Betony): Common throughout.

Veronicastrum virginicum (L.) Farw. (Culver's Root): Frequent throughout.

Solanaceae

**Solanum dulcamara* L. (Bittersweet Nightshade): R Incidental. Rare on disturbed margins.

Ulmaceae

**Ulmus pumila* L. (Siberian Elm): R Scattered throughout on dry hummocks and shrub thickets.

Umbelliferae

Angelica atropurpurea L. (Giant Angelica): R, L, SC Frequent in northwest, very rare elsewhere. (8 sites)

Cicuta bulbifera L. (Bublet-bearing Water Hemlock): R Scattered throughout in wet soil.

Cicuta maculata L. (Water Hemlock): Frequent throughout.

Oxypolis rigidior (L.) Raf. (Cowbane): Common throughout. This is the most ubiquitous fen umbel.

Sium suave Walt. (Water Parsnip): R Uncommon throughout.

Zizia aurea (L.) W. P. J. Koch (Golden Alexanders): Scattered throughout on dry hummocks and margins.

Urticaceae

Boehmeria cylindrica (L.) Sw. (False Nettle): Most frequent in extreme east.

Parietaria pensylvanica Muhl. ex Willd. (Pellitory): Incidental. Rare on hummocks.
Pilea fontana (Lunnell) Rydb. (Spring Clearweed): R, L Frequent throughout. (63 sites)
Pilea pumila (L.) Gray (Clearweed): Incidental. Rare on disturbed, wooded margins.
Urtica dioica L. (Tall Nettle): Frequent in north half. Becomes dominant following disturbance.

Valerianaceae

Valeriana edulis Nutt. ex T. & G. (Common Valerian): R, L, SC Scattered in central. (17 sites)

Verbenaceae

Verbena hastata L. (Blue Vervain): Common throughout, particularly on disturbed margins.

Violaceae

Viola lanceolata L. (Lance-leaved Violet): R Rare in south third on wet, sandy margins. (4 sites)
Viola nephrophylla Greene (Northern Bog Violet): Abundant throughout. The most ubiquitous fen violet.
Viola pallens (Banks ex DC.) Brainerd [*V. macloskeyi* F. E. Lloyd ssp. *pallens* (Banks ex DC.) C. L. Hitchc.] (Smooth White Violet): R Scattered in central. (15 sites)
Viola primulifolia L. (Primrose Violet): R, L Rare in east. (1 site)
Viola sagittata Ait. (Arrow-leaved Violet): Incidental. Infrequent on dry margins.

Vitaceae

Parthenocissus vitacea (Knerr) A. S. Hitchc. (Thicket Creeper): Scattered throughout on dry hummocks and margins.
Vitis riparia Michx. (Wild Grape): Rare on shrub thickets.

MONOCOTYLEDONS

Alismataceae

Alisma subcordatum Raf. (Common Water Plantain): Occasional on muddy margins.
Sagittaria latifolia Willd. (Common Arrowhead): Frequent throughout in wet soil.

Araceae
(including *Acoriaceae*)

Acorus calamus L. (Sweet Calamus): Scattered throughout.

Symplocarpus foetidus (L.) Salisb. ex Nutt. (Skunk Cabbage): R Scattered in extreme east. (3 sites)

Cyperaceae

Carex annectens (Bickn.) Bickn. (Yellow-fruited Sedge): Scattered throughout.
Carex bebbii Olney ex Fern. (Bebb's Sedge): Scattered throughout.
Carex buxbaumii Wahlenb. (Buxbaum's Sedge): Frequent throughout.
Carex comosa Boott (Bristly Sedge): R Scattered throughout in very wet soil.
Carex cristatella Britt.: Uncommon on margins.
Carex diandra Schrank: R, L A single old collection only (Eilers, 1971), no extant populations observed.
Carex frankii Kunth (Frank's Sedge): R, L Rare in southeast on dry fen margins.
Carex granularis Muhl. ex Willd.: NI Scattered in north and northwest, preferring mineral rich soils. (9 sites)
Carex hystericina Muhl. ex Willd. (Bottlebrush Sedge): Common throughout.
Carex interior Bailey (Inland Sedge): Common throughout.
Carex lacustris Willd.: R Scattered in north half.
Carex laeviconica Dew.: R, L Rare in southeast. (1 site)
Carex lanuginosa Michx. (Woolly Sedge): Common throughout.
Carex lasiocarpa Ehrh. var. *americana* Fern.: NI Scattered in central on very wet soils. (6 sites)
Carex leptalea Wahl.: NI, L, E Rare in south third, typically associated with eolian sands. (5 sites)
Carex normalis Mackenz.: Scattered throughout on margins.
Carex prairea Dew. ex Wood. (Fen Sedge): R, L Common throughout. (92 sites)
Carex rostrata Stokes var. *utriculata* (Boott) Bailey [*C. utriculata* Boott]: R, L Scattered throughout. Prefers very wet soil conditions. (5 sites)
Carex sartwellii Dew.: R, L Absent in southeast, scattered elsewhere.
Carex scoparia Schkuhr ex Willd. (Pointed Broom Sedge) scattered throughout.
Carex sterilis Willd.: NI, NS Rare in central. (7 sites)
Carex stipata Muhl.: Uncommon in southeast on muddy margins.
Carex stricta Lam. (Tussock Sedge): Abundant throughout.
Carex suberecta (Olney) Britt.: R Absent from northwest (?), common elsewhere.
Carex tetanica Schkuhr: R,L Scattered in north half. (16 sites)
Carex tribuloides Wahl.: R Uncommon throughout.
Carex vulpinoidea Michx. (Fox Sedge): Common throughout on disturbed margins.
Cyperus rivularis Kunth. [*C. bipartatus* Torr.] (Brook Sedge): R Scattered and rare along discharge streams and in low vegetation mats.
Eleocharis acicularis (L.) R. & S. (Needle Spike Rush): R Incidental. Collected once (Eilers, 1971), but no extant populations observed.
Eleocharis elliptica Kunth. (Fen Spike Rush): NI Frequent throughout. This is our most ubiquitous fen *Eleocharis*. (51 sites)
Eleocharis palustris (L.) R. & S.: Scattered throughout.
Eleocharis smallii Britt. (Small's Spike Rush): NI Scattered and rare.
Eriophorum angustifolium Honckeny (Narrow-leaved Cotton Grass): R, SC Absent from extreme southeast, frequent elsewhere. (68 sites)

Eriophorum gracile W. D. J. Koch (Slender Cotton Grass): R, L, E No extant populations observed, however, old collections exist (Eilers, 1971).
Eriophorum virginicum L. (Tawny Cotton Grass): NI, NS Very rare in central in *Sphagnum* dominated fen on eolian sand ridge. (1 site)
Rhynchospora capillacea Torr. (Hairy Beak Rush): NI, L, T Rare and scattered in north half, preferring mats of very low vegetation. (8 sites)
Scirpus cyperinus (L.) Kunth. (Wool Grass): Frequent throughout.
Scirpus fluviatilis (Torr.) Gray (River Bulrush): R Incidental. Rare in extreme south.
Scirpus validus Vahl. [*S. tabernaemontani* K. C. Gmel.] (Great Bulrush): Frequent throughout. Often found in fens with mats of low vegetation.
Scleria verticillata Muhl. ex Willd. (Vanilla Nut Rush): NI, L, E Scattered and rare in central. Is restricted to mats of low vegetation. (6 sites)

Gramineae

**Agrostis alba* L. [*A. gigantea* Roth.] (Redtop): Frequent throughout.
Agrostis hyemalis (Walt.) BSP. (Tickle Grass): Occasional throughout.
Andropogon gerardii Vit. (Big Bluestem): Uncommon in west half on dry hummocks.
Bromus ciliatus L. (Fringed Brome): R Occasional in north half. (7 sites)
Calamagrostis canadensis (Michx.) Beauv. (Blue Joint Grass): Abundant throughout.
Calamagrostis inexpansa Gray [*C. stricta* (Timm) Koel. ssp. *inexpansa* (Gray) C. W. Greene] (Bog Reed Grass): NI Rare and scattered in extreme north.
**Digitaria sanguinalis* (L.) Scop. (Smooth Crabgrass): Incidental. Rare on disturbed margins.
Echinochloa crus-galli (L.) Beauv. (Barnyard Grass): R Incidental. Rare on disturbed margins.
Festuca paradoxa Desv. (Large Fescue): R Scattered throughout. (6 sites)
Glyceria grandis S. Wats. (Reed Manna Grass): R Occasional in very wet soil along discharge streams.
Glyceria striata (Lam.) A. S. Hitchc. (Fowl Manna Grass): Abundant throughout.
Hierochloe odorata (L.) Beauv. (Vanilla Grass): R Scattered in north half.
**Hordeum jubatum* L. (Squirrel-tail Grass): Incidental. Rare on dry hummocks.
Leerzia oryzoides (L.) Sw. (Rice Cut Grass): Frequent throughout, often in disturbed sites.
Muhlenbergia glomerata (Willd.) Trin. (Fen Wild Timothy): R, L Common throughout. (102 sites)
Muhlenbergia mexicana (L.) Trin. (Leafy Satin Grass): R Common throughout.
Panicum boreale Nash [*Dicanthelium boreale* (Nash) Frackmann] (Northern Panic Grass): NI, E Rare in south central, preferring dry hummocks and moist sand margins. (4 sites)
Panicum implicatum Scribn. [*Dicanthelium acuminatum* (Sw.) Gould & C. A. Clark var. *fasciculatum* (Torr.) Frackmann]: Common throughout on dry hummocks and low vegetation mats.
Phalaris arundinacea L. (Reed Canary Grass): Native species extensively planted for pasture 'improvement' on disturbed sites, where it becomes dominant.

Phragmites communis Trin. [*P. australis* (Cav.) Trin. ex Steud.] (Common Reed Grass): R Rare and scattered in north third.
**Poa compressa* L. (Canadian Bluegrass): Occasional throughout on margins.
Poa palustris L. (Marsh Bluegrass): Rare in wet soil.
**Poa pratensis* L. (Kentucky Bluegrass): Common throughout on margins.
Sorghastrum nutans (L.) Nash (Indian Grass): Incidental. Rare on dry hummocks and margins.
Spartina pectinata Link (Slough Grass): Scattered throughout on margins.
Sphenopholis intermedia (Rydb.) Rydb. (Slender Wedge Grass): R Common throughout.
Sphenopholis obtusata (Michx.) Scribn. (Prairie Wedge Grass): R Rare and scattered throughout.

Iridaceae

Iris virginica L. var. *shrevei* (Sm.) Anders. (Blue Flag): Common throughout.

Juncaceae

Juncus canadensis J. Gay ex Laharpe (Canadian Rush): R Incidental. Occasional on margins.
Juncus dudleyi Wieg. (Dudley's Rush): Common throughout.
Juncus nodosus L. (Joint Rush): R Absent from extreme southeast, scattered elsewhere where it is most typically found in mats of low vegetation.
Juncus tenuis Willd. (Path Rush): Incidental. Occasional on disturbed fen margins.
Juncus torreyi Coville (Torrey's Rush): R Incidental. Rare on fen margins.

Juncaginaceae

Triglochin maritimum L. (Common Bog Arrow Grass): NI, L, T Rare in northwest. (2 sites)
Triglochin palustre L. (Slender Bog Arrow Grass): NI, L, T Rare in central. (2 sites)

Lemnaceae

Lemna minor L. (Small Duckweed): Incidental. Uncommon in discharge streams.
Spirodela polyrrhiza (L.) Schleid. (Great Duckweed): Incidental. Uncommon in outlet streams.

Liliaceae

Hypoxis hirsuta (L.) Cov. (Yellow Star Grass): Incidental. Occasional on dry hummocks and margins.
Lilium michiganense Farw. (Michigan Lily): Incidental. Rare on dry hummocks and margins.
Melanthium virginicum L. (Bunchflower): R, L Incidental. Observed only once on badly degraded site in south central.

Smilacina stellata (L.) Desf. [*Maianthemum stellatum* (L.) Link] (Starry False Soloman's Seal): Incidental. Rare on dry hummocks and margins.
Zygadenus elegans Pursh (White Camass): R Scattered in north half on margins.

Orchidaceae

Cypripedium candidum Muhl. ex Willd. (White Lady's Slipper): R, L, T Rare in northwest half. (3 sites)
Cypripedium parviflorum Salisb. (Small Yellow Lady's Slipper): NI, NS Rare in central. (2 sites)
Cypripedium pubescens Willd. (Large Yellow Lady's Slipper): R, L Occasional in northeast.
Cypripedium reginae Walt. (Showy Lady's Slipper): R, L, E Rare in central. (1 site)
Cypripedium ×*andrewsii* A. M. Fuller (Andrew's Lady's Slipper): NI, L Rare in central. (1 site)
Cypripedium ×*favillianum* Curtis (Favill's Lady's Slipper): NI, NS Rare in central. (1 site)
Habenaria flava (L.) R. Br. var. *herbiola* (R. Br. ex Ait. f.) Ames & Correll [*Platanthera flava* (L.) Lindl. var. *herbiola* (R. Br. ex Ait. f.) Leur] (Green Orchid): R, L, E Rare in south third on wet, sandy margins. (2 sites)
Habenaria hyperborea (L.) R. Br. [*Platanthera hyperborea* (L.) Lindl.] (Northern Fringed Orchid): NI, L, T Very rare in north. (1 site)
Habenaria praeclara (Sheviak & Bowles) Cronq. [*Platanthera praeclara* Sheviak & Bowles] (Prairie Fringed Orchid): R, L, E Incidental. Rare in central. (1 site)
Habenaria psycodes (L.) Spreng. [*Platanthera psycodes* (L.) Lindl.] (Purple Fringed Orchid): R, L, T Scattered and rare throughout. (5 sites)
Liparis loeselii (L.) Rich. (Fen Twayblade): R, L Scattered throughout. (12 sites)
Spiranthes cernua (L.) Rich. (Nodding Lady's Tresses): Scattered throughout.
Spiranthes lucida (H. H. Eat.) Ames (Early Lady's Tresses): NI, NS, E Very rare in northeast. (1 site)

Typhaceae
(including *Sparganiaceae*)

Sparganium eurycarpum Engelm. ex Gray (Common Bur Reed): R Occasional throughout in very wet soil.
Typha angustifolia L. (Narrow-leaved Cattail): R Frequent thro ughout.
Typha latifolia L. (Common Cattail): Common throughout.

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NOMENCLATURAL NOTES IN NYMPHAEACEAE FOR THE NORTH AMERICAN FLORA

JOHN H. WIERSEMA AND C. BARRE HELLQUIST

ABSTRACT

In conjunction with a study of the Nymphaeaceae in North America, the taxonomy and nomenclature of three taxa is reviewed. Two new combinations are provided at subspecific rank for two taxa sometimes treated as species, one for *Nymphaea tuberosa* Paine and one for *Nuphar rubrodisca* Morong, and both are lectotypified. A neotype is selected for *Nymphaea advena* Aiton which serves to maintain usage of Aiton's epithet for a widespread taxon of *Nuphar*.

Key Words: *Nuphar, Nymphaea,* water-lilies, cow-lilies, spatterdock

Research on the genera *Nymphaea* and *Nuphar* of the Nymphaeaceae has revealed that the following nomenclatural adjustments are necessary for a flora of North America treatment.

Nymphaea odorata Aiton subsp. *tuberosa* (Paine) Wiersema & Hellquist, *comb. nov.*

Nymphaea tuberosa Paine, Annual Rep. State Cabinet Nat. Hist. New York 18: 184 (Cat. pl. Oneida Co. 132). 1865. TYPE: UNITED STATES. New York: S. shore of Lake Ontario, 1865, *Paine s.n.* (LECTOTYPE: K). See discussion.

Nymphaea odorata, which is distributed throughout eastern North America, is a polymorphic species. In and around the Great Lakes region, where the plants here designated as subsp. *tuberosa* are found, two predominate forms can be observed. In the southern part of the range of subsp. *tuberosa* where subsp. *odorata* is absent, e.g., in Iowa, Illinois, Indiana, Ohio, and somewhat to the north and east, plants of subsp. *tuberosa* are easily distinguished morphologically from subsp. *odorata* (see accompanying key). Further north where their ranges overlap occasional populations are intermediate in morphology or more rarely populations may include plants referable to both subspecies as well as intermediate plants. The intermediates exhibit a range of variation spanning the morphological gap between the two subspecies and, in some cases at least, display no evidence of reduced fertility. Although traditional treatments distinguished the two forms at specific rank, several recent floristic works (e.g., Voss, 1985; Glea-

son and Cronquist, 1991) have combined them into one variable species without further distinction. While calling attention to this taxonomic problem, field studies from within this region (Monson, 1960; Williams, 1970; Bayly and Jongejan, 1982) have not sufficiently accounted for the observed variation. These studies suggest that some variability may be induced by environmental conditions; however, we have observed both extremes growing together under seemingly identical conditions. Such populations require more detailed study before this variation is fully understood. Artificial hybridization studies and/or molecular approaches may also aid in clarifying this relationship.

Based on existing knowledge, we believe the geographic patterning of the overall variation and the usefulness of retaining a separate status for those forms previously classified as *Nymphaea tuberosa* justifies the recognition of two subspecies, as distinguished below. While useful in separating the two extremes in this morphological continuum, the key is of limited use in identifying intermediate plants. Compounding the problem of identification is the fact that key characters are often poorly represented on herbarium material. Populations containing intermediate plants are known from Minnesota, Wisconsin, Michigan, New York, Vermont, and southern Ontario and Quebec and until better understood are best treated as *Nymphaea odorata* without regard to subspecies.

1. Petioles not striped; blades usually reddish-purple (occasionally green) abaxially; seeds 1.5–2.5 mm long ..... subsp. *odorata*
1. Petioles with brown-purple stripes; blades green or faintly purple abaxially; seeds mostly 2.8–4.5 mm long ..... subsp. *tuberosa*

Paine (1865) cited a number of localities for *Nymphaea tuberosa* but failed to designate a holotype. To fix the application of his name it is appropriate to select a lectotype. Conard's (1905) listing of "*Nymphaea tuberosa* Paine (1865), fid. specimen coll. Paine on S. shore of Lake Ontario, from hb. A. Gray, in hb. Kew" is considered not to represent an effective lectotypification as it does not satisfy the requirements of Article 8.3 of the International Code of Botanical Nomenclature (Greuter et al., 1988). The spec-

imen at Kew contains a leaf, two flowers, and a developing fruit and matches our concept of subsp. *tuberosa*; it is here formally designated as lectotype.

Nuphar lutea (L.) Smith subsp. *rubrodisca* (Morong) Hellquist & Wiersema, *comb. nov.*

Nuphar rubrodiscum Morong, Bot. Gaz. 11: 167–168. 1886. TYPE: UNITED STATES. Vermont: at the mouth of Lewis Creek, Lake Champlain, Ferrisburgh, 5 Aug 1885, *Morong s.n.* (LECTOTYPE: NY). See discussion. *Nymphaea rubrodisca* (Morong) E. Greene, Bull. Torrey Bot. Club 15: 84. 1888.

While working with the genus *Nuphar* Smith, we became aware of the need for a new combination in addition to those at subspecific rank previously made by Beal (1956). *Nuphar lutea* subsp. *rubrodisca*, which Beal treated under the hybrid formula *N. lutea* subsp. *pumila* (Timm) E. O. Beal × *N. lutea* subsp. *variegata* (Durand) E. O. Beal and most likely of hybrid origin, is producing viable seed and is found in areas far removed from either of the probable parents. It differs from the other two subspecies in a number of characteristics, as detailed in our flora treatment, and in accordance with Article H.3.4 Note 1 and Example 3, we prefer to treat this as an additional subspecies. As no name at subspecific rank exists for this taxon, Morong's epithet, which has most commonly been applied to it, can be retained.

As Morong failed to designate a holotype, a lectotype is selected. In his original publication, Morong discussed his study of this taxon during the summer of 1885 along Lake Champlain at Ferrisburgh, Vermont near the mouths of Lewis and Little Otter creeks. Following the description, he lists "Lake Champlain, Vt." as the type locality. Three sheets of this taxon from Morong's original herbarium now at NY pertain to this study. One sheet stamped "MORONG HERBARIUM" contains 3 leaves and 3 mounted and several unmounted fruits and bears two labels: 1) "lvs. of N. rubrodiscum, Ferrisburgh, Vt., Aug. 5, 1885" and 2) "N. rubrodiscum fruit, Ferrisburgh, Aug. 11." A second sheet stamped "MORONG HERBARIUM" and "BRITTON HERBARIUM" contains 4 leaves, 1 mounted flower, and 3 mounted and some unmounted fruits and bears 4 labels: 1) "Leaves of N. rubrodiscum, Lewis Creek, Ferrisburgh, Vt."; 2) identical with *1*;

3) "N. rubrodiscum Morong, Lewis Creek, Ferrisburgh, Vt.; Aug. 6, 1885"; and 4) "N. rubrodiscum, Lewis Creek, Ferrisburgh, Vt., Aug. 11, 1885." On all the above labels the epithet *luteum* has been overwritten with *rubrodiscum.* The third sheet stamped "MORONG HERBARIUM, property of BARNARD COLLEGE" contains 1 leaf, 1 flower, and 2 fruits and bears a single label: "Nuphar rubrodiscum Morong, N. luteum Sm.?. At the mouth of Lewis Creek, Lake Champlain, Ferrisburgh, Vermont. Leg. T.M. 18 5/8 85." This sheet is accompanied by a lengthy note written by Morong the content of which is entirely reproduced in the protologue. On this sheet the provisional name *Nuphar rubrum* has been replaced with *N. rubrodiscum* both on the label and the note. While all three sheets match the original description, this third sheet is the only one which appears to represent a single gathering. It is also the most completely labelled and contains both flowers and fruits. It has been selected as lectotype.

Nuphar lutea (L.) Sm. subsp. *advena* (Aiton) Kartesz & Gandhi, Phytologia 67: 463. 1989, "*advenum.*"

Nymphaea advena Aiton, Hort. kew. 2: 226. 1789. TYPE: UNITED STATES. Pennsylvania: Philadelphia, tidal marsh along Darby Creek in John Heinz National Wildlife Refuge at Tinicum, 24 July 1993, *J. H. Wiersema & A. E. Schuyler 2372* (NEOTYPE: PH; ISONEOTYPES: US, BM). See discussion. *Nuphar advena* (Aiton) W. T. Aiton, Hort. kew. ed. 2, 3: 295. 1811.

In conjunction with this study, we have been investigating the typification of *Nymphaea advena* Aiton, which has commonly been applied to a taxon of North American *Nuphar,* as *Nuphar advena* (Aiton) W. T. Aiton or *Nuphar lutea* subsp. *advena* (Aiton) Kartesz & Gandhi. The original publication (Aiton, 1789) is a "catalogue of the plants cultivated in the Royal Botanic Gardens at Kew." As is typical of most early botanical publications, no specimens were directly cited in the protologue of *Nymphaea advena.* The native distribution was given as "North America," the phrase name *Nymphaea floribus flavis* Clayton in Gronovius, Flora virginica 164. 1743 was cited, and it was said to have been introduced by Mr. William Young in 1772. According to Stafleu and Cowan (1976), type material for both Hortus kewensis and

Flora virginica is deposited at BM. However, from correspondence with the herbaria of both Kew (G. L. Lucas, pers. comm.) and British Museum (R. Vickery, pers. comm.) it is clear that no material of the Kew cultivation or the John Clayton collection, which served as the basis for the Gronovius phrase name, can be located.

The original description appears to combine characteristics of two taxa, *Nuphar advena* and *Nuphar variegata* Durand, which we distinguish at the rank of subspecies following Beal (1956). The traits of semiterete petioles and purple-colored sepals and stamens best apply to *Nuphar lutea* subsp. *variegata* (Durand) E. O. Beal while the emergent leaves clearly indicate subsp. *advena*. Most early users of Aiton's name (Poiret, 1798; Willdenow, 1799, 1809; Michaux, 1803; Sims, 1803; Martyn, 1807; de Candolle, 1821; Torrey and Gray, 1838; Planchon, 1853; Morong, 1886) did not recognize the distinctions between the two taxa. Pursh (1814) distinguished the two, but misapplied the European *Nuphar lutea* to what was named *Nuphar variegata* in 1866. Bigelow (1824) and Hooker (1829), while noting the differences between the northern and southern plants, continued to treat both as a single taxon. Hooker's comment that "Dr. Graham and myself have long observed that the *N. advena,* as cultivated in our gardens, has the leaves sometimes floating, sometimes rising above the water" indicates that both taxa were introduced to Europe. Whether or not this was the case some 40 years earlier when the original description was published by Aiton is not known. In any event, none of these early authors succeeded in typifying *Nymphaea advena*.

The relationship between the two taxa was clarified by Miller (1902). Though he stated that the type locality of *Nymphaea advena* was probably Philadelphia, Miller failed to lectotypify the name. In their revision, Miller and Standley (1912) listed the type locality as "vicinity of Philadelphia, Pennsylvania" but cited no type specimen. Beal's 1956 revision accepted *Nuphar lutea* subsp. *variegata* for the floating-leaved northern taxon and *Nuphar lutea* subsp. *macrophylla* (Small) E. O. Beal for the emergent-leaved southern one, listing Aiton's name as a partial synonym of both. For nomenclatural reasons, Kartesz and Gandhi (1989) replaced subsp. *macrophylla* with subsp. *advena* (Aiton) Kartesz & Gandhi. To this day, however, Aiton's name has never been properly typified. Since Miller it has consistently been applied to the emer-

gent-leaved taxon and to preserve this usage the name must be typified on that element.

The supposition that the type locality should be Philadelphia was presumably based on that being the home of the William Young referred to by Aiton as having introduced the plant to England in 1772. According to Harshberger (1917), William Young, Jr. (1742–85) of Philadelphia, in his capacity as botanist to the Queen of England, departed Philadelphia for England in November of 1771, no doubt carrying the *Nuphar* material he is credited with having introduced the following year. A 1772 letter from Dr. John Fothergill of London to Humphrey Marshall of Philadelphia, reported by Rhoads (1916), reports receipt of material of *Nelumbo* from William Young, Jr. that same year. Young is known to have carried material from the Carolinas abroad but this was in 1768 and 1769 (Harshberger, 1917). As he did not apparently make any further trips to the southern states following his return to Philadelphia in 1770, his 1772 introductions to England would seem to have been collected near to his home in Philadelphia.

In his flora of the Philadelphia area, William Barton (1818) applied *Nuphar advena* to an emergent-leaved taxon which was said to be abundant "on the marshy shores of the Delaware, Schuylkill, and all other waters in our neighborhood, covering the shores for miles together in extent" and in terms of current usage this appears to be the desired application of the name. Young's estate was reportedly adjacent to that of John Bartram, which bordered the Schuylkill River (Harshberger, 1917). A recent field trip in the company of A. E. Schuyler provided an opportunity to study *Nuphar* in the Philadelphia area on both sides of the Delaware River near the mouth of the Schuylkill. Large populations still exist in some protected areas, probably remnants of the formerly extensive distribution. Much of the area remains under tidal influence as would have been the case in Young's time.

The populations consist of strongly emergent plants, almost completely so at low tide, which have flowers mostly with parts variously tinged with reddish-purple. Such coloration is lacking over most of the range of the taxon commonly referred to as *N. advena,* but is characteristic of *N. variegata,* which is found at nearby sites in southern New Jersey. A full range of intermediate plants for those characters which normally distinguish the two

taxa can be observed in other southern New Jersey localities. Though the populations in the immediate vicinity of Philadelphia display some degree of intermediacy, their overall morphology compares well with *N. advena* as the name has been applied by most authors. One of our collections near the mouth of the Schuylkill thus serves as a suitable neotype.

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J. H. W.
UNITED STATES DEPARTMENT OF AGRICULTURE
AGRICULTURAL RESEARCH SERVICE
BUILDING 011A, BARC-WEST
BELTSVILLE, MARYLAND 20705-2350

C. B. H.
NORTH ADAMS STATE COLLEGE
BOX 9145
NORTH ADAMS, MASSACHUSETTS 01247

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LIFE HISTORY OF SHOOTS OF *CAREX COMOSA* F. BOOTT.

JOHN M. BERNARD AND FRANZ K. SEISCHAB

ABSTRACT

Carex comosa shoots have a life history which varies depending on their time of emergence. Shoots that emerge in spring, summer or early autumn develop flower initials before winter, flower the following year, then die in August, having lived 240–420 days. Shoots that emerge in late autumn do not develop flower initials, remain vegetative the next summer, then develop flower initials in the second autumn. These shoots flower and die the following summer, having lived for up to 700 days. Few shoots live their maximum time and mortality is 90% in some cohorts. Mortality patterns indicate that shoots die at a constant rate throughout the year.

Key Words: *Carex,* life history, ramets, central New York

INTRODUCTION

Many temperate zone wetland ecosystems are dominated by clonal *Carex* plants. Such plants (genets) are capable of producing large numbers of shoots (ramets) through continuous reiteration of modules. Each shoot is typically separated by a spacer organ, usually a rhizome.

Different clonal sedge species have evolved different life history adaptations. Bernard (1990), in his review of *Carex,* noted three basic patterns of growth based on behavior of the spacer organ. He pointed out that some species have spacers which are short, resulting in tight clumps of shoots, while others have long rhizomes and place shoots at a distance from the parent shoot. The third and probably most common type is found in those shoots that produce both long and short rhizomes, resulting in loose clumps of shoots connected to other loose clumps through the rhizomes.

There has been a relatively large number of studies on *Carex* species exhibiting the latter two strategies, among them those by Bernard (1975, 1976), Bernard and Gorham (1978), Bernard and MacDonald (1974), Callaghan (1976, 1990), Costello (1936) and Ratliff (1983) but few on those that produce only short spacers and grow in clumps. Examples are the studies of David and Kelcey (1985) on the *C. muricata* L. complex, Schmid (1984) on *C. flava*

L., Taylor (1956) on *C. flacca* Schreber, and Bernard and Fiala (1986) on *C. comosa* Boott.

Carex comosa is a large clump-forming species whose shoots produce short rhizomes only. It is found scattered in disturbed areas of wetlands. Bernard and Fiala (1986) found that the smallest clones were made up only of vegetative shoots, but as the clones grew larger the flowering percentage increased to a maximum of almost 70% in the largest 100-shoot clones. The shoot/root ratio also increased as the clones expanded in size. From their study, they labelled *C. comosa* a long-lived fugitive species which invades gaps in wetlands, grows vegetatively for the first years, then flowers heavily when larger. This adaptation enables *C. comosa* to invade a gap, increase in ramet numbers and hold the gap for a decade or more while producing large crops of seeds, some of which may find new gaps to invade.

The purpose of this study was to determine life history and demographic patterns in shoots of *Carex comosa* and to determine if there are phenological differences in plants growing in different sites.

METHODS

Data were collected from three different study areas, two in the Cumming Nature Center, Naples, New York and one in Inlet Valley, Ithaca, New York. The Inlet site was the same one used by Bernard and Fiala (1986) and was dominated by *Sparganium eurycarpum* Engelm. Botanical nomenclature follows Gleason and Cronquist (1991). A small stream flowed through the site with a row of willows (*Salix* sp. L.) bordering one side. One of the Nature Center sites was just downstream from an active beaver (*Castor canadensis*) dam. The water table was just at the surface of the soil during the growing season; the vegetation was a mixture of many species including *Typha latifolia* L., *Carex lacustris* Willd. and *Leersia oryzoides* (L.) Swartz. There was a considerable number of trees at the site and tree branches were common on the ground. The second Nature Center site was upstream from the beaver dam along the pond shore. This site had less herbaceous cover with a few scattered alders (*Alnus incana* L. Moench.). The water table was somewhat lower and the organic soil more consolidated than at the site below the dam.

All shoots of *Carex comosa* in the 14 clones growing in the two

sites at Cumming Nature Center were tagged with a numbered plastic tag in the autumn of 1983 or spring of 1984. The length of all shoots/clone were measured then and at subsequent visits at approximately monthly intervals during the growing season until autumn 1985. All shoots tagged on each date became part of a cohort. Notes on the health of shoots and whether they were in vegetative or flowering condition were made at each visit. New shoots were tagged as they emerged. In order to determine if differences in mean number of shoots per plant above and below the beaver dam at the Nature Center were significant, a sample *t*-test was conducted.

In a separate part of the study, all shoots in three clones were tagged on November 5, 1983 in Inlet Valley. There were 64 shoots in the three clones varying in length from 3.5 cm to over 100 cm. All shoots were placed in four cohorts, defined differently than those above; cohort 1 was made up of the smallest shoots which had just emerged above ground plus four additional shoots that emerged after November 5. Cohorts 2 and 3 were shoots which had emerged in summer and early autumn and grew to heights of 10–20 cm by November. Cohort 4 was made up of shoots over 30 cm long; most had a cluster of dead leaves at the shoot bases. These clones were visited four times between November 5 and June 22, 1984. At each visit, other non-tagged clones were harvested. These were brought back to the laboratory, individual shoots measured, then dissected to determine if the shoots had flowering initials present. All shoots were dried and weighed after dissection.

RESULTS

Table 1 presents data on the total number of shoots in each of nine clones located at Site 1 at the Nature Center, downstream from the beaver dam. Shoot numbers in five of the clones increased from 80 to 400%, one clone remained the same, and three declined over the 25-month period of study. The total number of shoots in all clones went from 77 to 134 after one year, then increased slightly to 139 after the second year, for a total gain of 80%. Shoot number during both summers increased about 35% but varied dramatically during the two winter periods. From September 1983 to May 1984, shoot numbers increased 28%, but from September 1984 to May 1985, they decreased by 22%. Thus,

Table 1. Number of shoots/clone and total numbers in nine clones of *Carex comosa* sampled over a two-year period. The site was located in a wetland just downstream from a beaver dam (Site 1).

	1983	1984		1985		9/83–10/85
Clone	9/19	5/21	9/17	5/24	10/17	% Change
1	5	10	13	17	25	400
2	7	15	15	10	25	257
3	8	10	17	16	19	137
4	15	13	28	21	28	87
5	15	20	29	22	27	80
6	4	7	10	5	4	0
7	9	9	8	6	7	−22
8	6	7	9	4	2	−66
9	8	7	5	3	2	−75
Totals	77	98	134	104	139	81%

although the average shoot percentage gain was 80% over two years, almost all the gain was during the first year; little change occurred during the second year. It is important to note that four of the clones were probably dying, two having two shoots remaining, and two having the same number or fewer shoots than at the beginning of the study.

Table 2 presents data for five clones growing at Site 2 along the edge of the pond upstream from the beaver dam. All clones increased at least 220% in total shoot numbers from May 1984 to October 1985, the average being 445%. Although mortality in winter was 18%, almost the same as clones at Site 1, emergence in summer was heavy; clones gained 152% from May to October 1985, a rate similar to the 164% growth of the previous summer.

Table 2. Number of shoots/clone and total numbers in five clones of *Carex comosa* at Site 2, located along the edge of a beaver pond.

	1984		1985		5/84–10/85
Clone	5/21	9/17	5/12	10/17	% Change
1	5	20	16	57	1040
2	5	19	16	29	500
3	6	10	13	34	466
4	6	13	11	20	233
5	9	20	11	29	222
Totals	31	82	67	169	445%

Table 3. Cumulative gains and losses and percentage change of *Carex comosa* shoots in nine clones at Site 1 and five clones at Site 2. Note: births and deaths are cumulative for each period; for example, between 5/21/84 and 7/3/84, 34 new shoots emerged and 12 died.

	Site 1				Site 2			
Date	Births	Deaths	Total Shoots	% Turn-over	Births	Deaths	Total Shoots	% Change
9-19-83			77					
5-21-84	36	15	98	20			31	
7-3-84	70	27	120	18	9	1	39	25
7-30-84	86	52	111	−8	18	3	46	18
8-21-84	127	77	127	14	51	6	76	65
9-17-84	160	103	134	6	65	14	82	7
5-24-85	186	159	104	−22	80	44	67	−18
6-24-85	202	163	116	12	136	55	112	67
7-23-85	252	170	159	37	159	66	124	10
8-26-85	286	211	152	−4	229	88	172	38
10-17-85	339	277	139	−9	308	170	169	−1

In comparison to Site 1 clones, the number of shoots in all Site 2 clones had at least doubled and one had increased over 10 times.

Shoot turnover for both sites is shown in Table 3 which gives the cumulative gains and losses during the sampling period. At Site 1, from September 1983 to October 1985, the total shoots increased from 77 to 139 but a total of 339 new shoots had emerged and 277 had died. At Site 2, total shoot numbers were 31 in May 1984 and increased to 169 in October 1985. Again, significant shoot turnover occurred with 308 shoots emerging and 170 dying.

Shoot mortality during the two winter periods varied during the study. During the first winter at Site 1, only 15 shoots died but 36 new shoots emerged, resulting in a 20% increase. In contrast, during the second winter, plants had high mortality with relatively low emergence resulting in a total loss of 22% of all shoots in the nine clones.

Clone numbers at Site 2 (Table 3) showed a somewhat different picture. Plant mortality over winter was high (54%), but emergence during the following spring was somewhat higher, resulting in a decline of 18% in total shoot numbers over winter.

Figure 1 shows the time of emergence for all cohorts of shoots in nine clones making up the population at Site 1 on July 23,

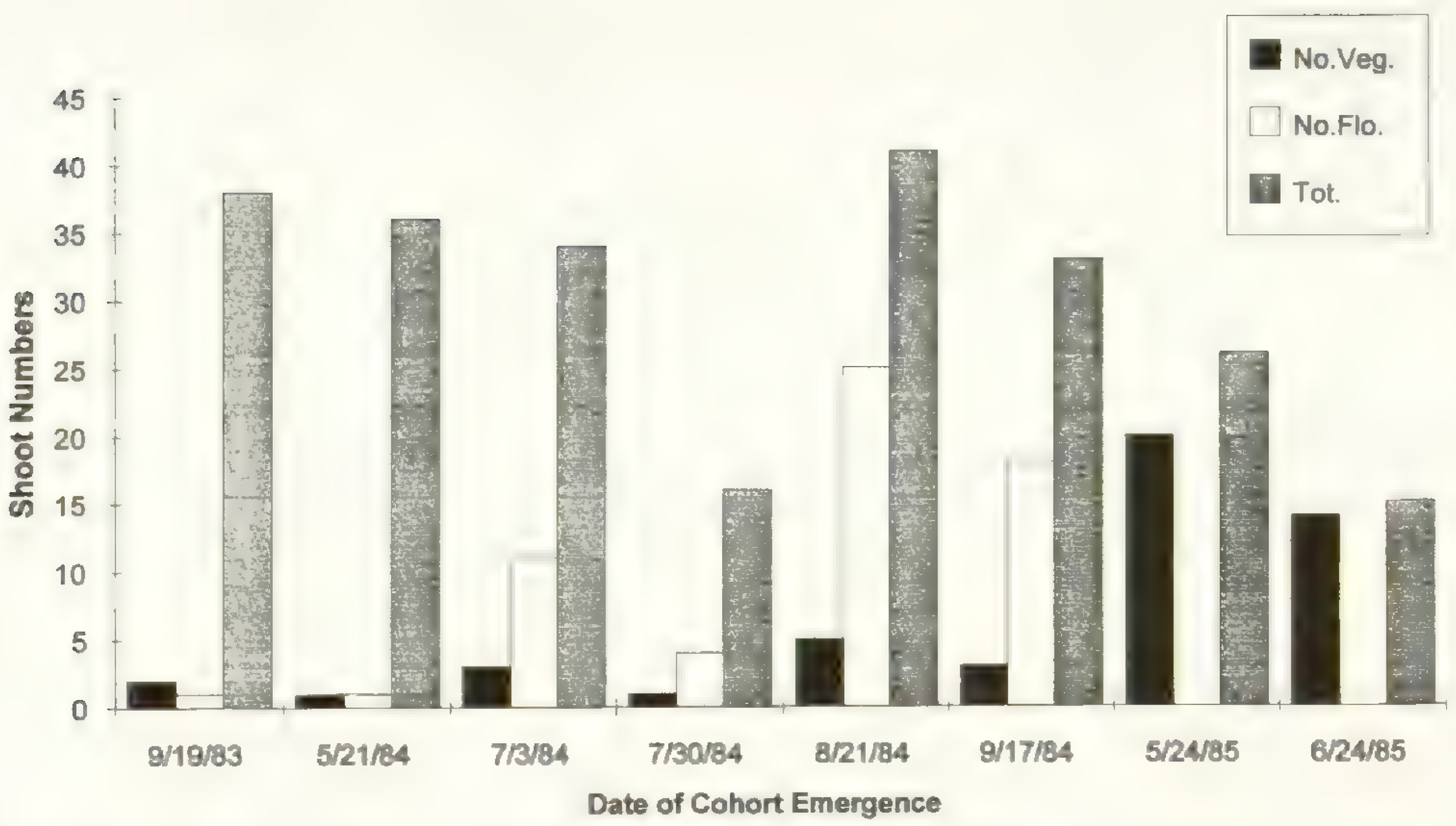

Figure 1. Age structure of 109 shoots in nine clones of *Carex comosa* on July 23, 1985. The total number of shoots originally tagged (shaded bars) in each of the dated cohorts is shown as is the number of vegetative (black bars) and flowering (open bars) shoots still alive.

1985. Bars represent the original number of shoots in each cohort (shaded) and the number of vegetative (black) and flowering shoots (open) still remaining at the end of the study. The oldest cohorts (9/1/83, 5/21/84, 7/3/84, 7/30/84) had very high mortality; few

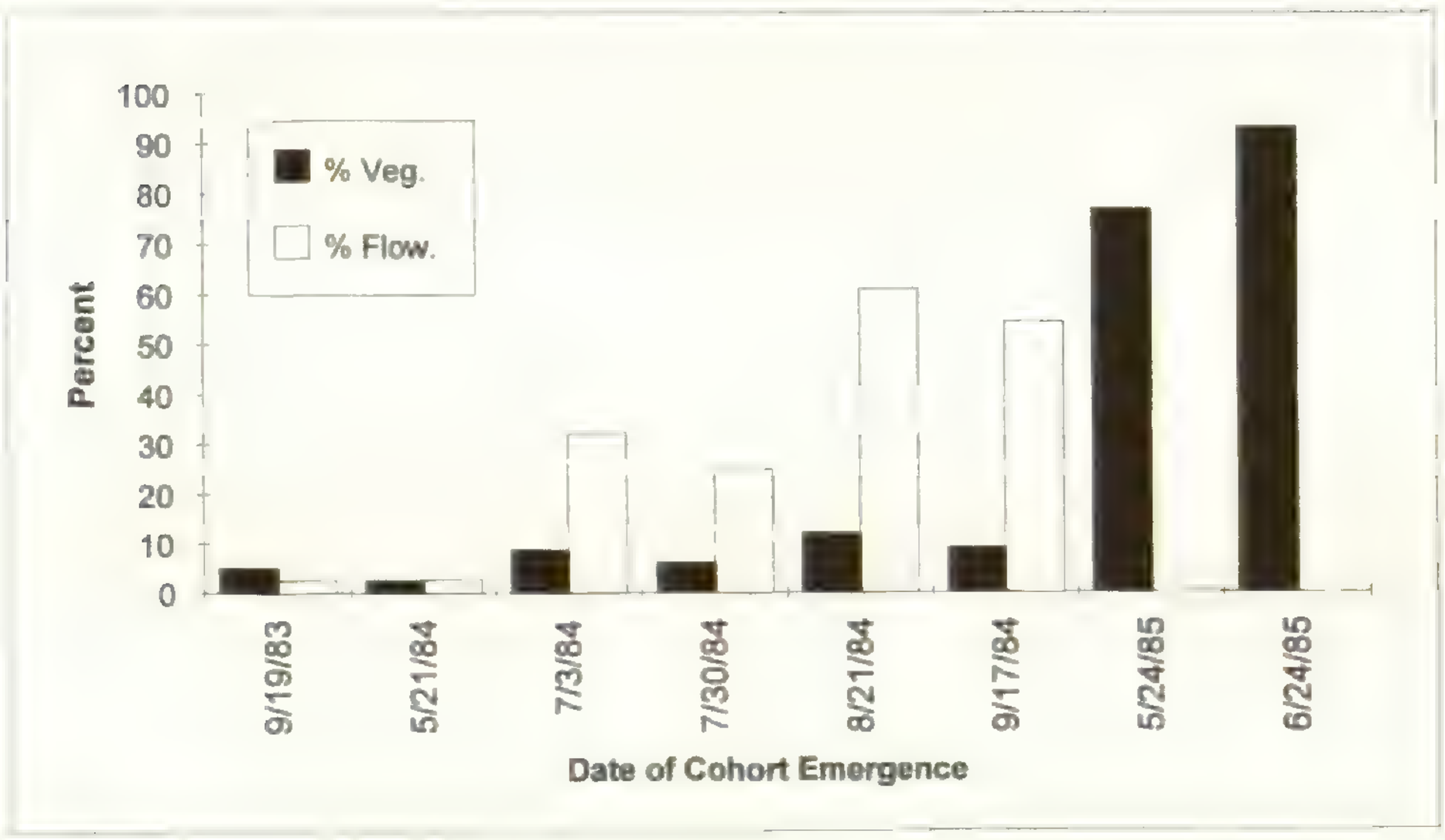

Figure 2. Percentage of vegetative (black bars) and flowering shoots (open bars) of *Carex comosa* remaining on July 23, 1985 from original number in the cohorts.

Table 4. Number of shoots in four cohorts of overwintering clones of *Carex comosa* at the Inlet Valley site.

	1984	1985		
Cohort	1/15	3/10	4/29	6/22
1	11	15	15	14*
2	25	26	26	26*
3	15	15	15	15*
4	13	13	12	6*
Totals	64	69	68	61

* Denotes shoots in flower.

shoots remained from the original number that had emerged. Mortality was less in the second 1984 cohort, and most that lived, flowered. None of the 1985 shoot cohorts flowered. Figure 2 gives percentages of vegetative and flowering shoots in the eight cohorts still living on July 23, 1985. The two oldest cohorts of autumn 1983 and May 1984 had over 90% shoot mortality; about half the survivors flowered. The rest of the 1984 cohorts had higher percentages living and most were flowering shoots. The youngest shoots of the 1985 cohorts were all vegetative and although having emerged only 1–2 months before July had considerable mortality, the June cohort having a 7% mortality.

Recently emerged shoots were all vegetative, but older cohorts, with the exception of the September 1983 cohort, had mostly flowering shoots. At the conclusion of the study, two shoots two years old were still in a vegetative condition, and 55% of shoots in all clones had flowered. Mortality patterns described a type II survivorship curve, a pattern to be expected of an opportunistic early successional species (Deevey, 1947).

In a separate part of the study, three clones were tagged in late autumn in the Inlet Valley site near Ithaca and followed during the winter and early spring. There were 64 shoots in the three clones tagged in November (Table 4); four additional shoots emerged in cohort 1 by March 10 and one additional larger shoot was tagged and placed in cohort 2. Of the total 69 shoots, 61 survived until June 22, with one shoot in cohort 1 and six of the original 13 in cohort 4 dying. The shoots that survived until June in all four cohorts averaged about 102 cm in length and all flowered.

In addition to the shoots placed in the four cohorts, almost all shoots in cohorts 2 and 3 produced one or more small axillary

shoots, all less than 3 cm long in March; at harvest in June these axillary shoots accounted for the largest percentage of vegetative shoots in each clone since none flowered. Cohort 1 and cohort 4 shoots did not produce any axillary shoots over winter during this study. We found that 37 of the 107 shoots harvested (35%) produced axillary shoots after November 5, a percentage about twice that of shoots in cohorts 2 and 3 of the tagged clones. Some of the harvested shoots which were old enough to have produced axillary shoots did not. These were all either smaller than average size, had brown meristems, or were infected with *Diptera* larvae.

DISCUSSION

Maximum length of life for single shoots of various *Carex* species is extremely variable. Some, such as *Carex lacustris,* live 12 months (Bernard, 1975); others such as *C. rostrata* may live for about 18–24 months in the temperate zone (Bernard, 1976) but longer, up to 60 months, in oligotrophic sites in northern Sweden (Solander, 1983). Many arctic and alpine tundra species also live for up to 60 months (Alexeev, 1988; Hultgren, 1988), as do some montane species. A particularly good example of long-lived shoots was found in *C. nebraskensis* Dewey, some of which lived for 96 months in alpine habitats of the Sierra Nevada Mountains in California (Ratliff, 1983).

Few *Carex* shoots live their maximum possible time and annual mortality is usually at least 80% in temperate sites although lower in arctic sites. Life spans are variable even in shoots in the same cohort, ranging, for example, from only 12 days to over 750 days in *C. lasiocarpa* Ehrh. (Bedford et al., 1988). Bedford et al. (1988) found, as did we, that shoots die at a constant rate, a situation also shown in other studies of *Carex* (Bernard, 1990). Shoots that emerge in late autumn or early winter have the longest possible life span in comparison to spring or summer emerged shoots but these differences are not as different as they at first appear. If one subtracts the approximately 140 days of winter from the autumn-emerged shoots the average life span becomes less variable. For example, shoots emerging in late autumn live for 670–700 days or so, the longest of all possible life spans, while spring shoots live for perhaps 550 days. Subtracting the 140 days of winter from the autumn shoots gives them approximately the same life span as spring shoots. It is the same situation described by Bedford et

al. (1988), who noted that both autumn and spring emerged shoots of *C. lasiocarpa* were part of the same cohort, the shoots not emerging until spring were already formed but were dormant below ground during the winter.

There is extremely heavy shoot turnover depending in part on whether or not individual clumps grew well. This has also been found in other *Carex* species. Bartlett and Noble (1985), Noble et al. (1979), Bernard (1990) and Callaghan (1976) all noted that at a time of favorable growth conditions, more shoots are produced than are needed for replacement; when the environment worsens, they die back. Thus, the better the environment for growth, the more emergence. When conditions become less suitable, greater than average mortality occurs. This mortality does not happen in more northern sites; Solander (1982) found little mortality in *C. rostrata* in her arctic study, owing probably to the low nutrient status of her site.

Mortality patterns did not match well in the years of study. During the first winter, clones showed low shoot mortality at both Nature Center sites but during the second winter clones had very high mortality, especially at Site 1. This may have been due to a high water table at Site 1 during the second winter; the water table at Site 2 did not vary to the same extent. The high second-year mortality at Site 1 had a profound effect on individual clones, some of which did not recover.

Flowering percentages in clumps varied for two reasons. First, size of clumps was important. Bernard and Fiala (1986) found that shoots in the smallest (and probably youngest) clones did not flower while the largest clones had as many as 67% of their shoots in flower. Second, we found in this study that during winter vegetative meristems of some shoots were either dead or affected by *Diptera* larva. These conditions obviously affect expected flowering percentages.

Bernard and Fiala (1986) noted that *Carex comosa* had the characteristics of an opportunistic early successional species, invading open sites, growing rapidly and then flowering. It also had characteristics that allowed it to live for a long time in a site favorable for growth. The shoot life history patterns found in this study allow this species to both compete for favorable sites while at the same time producing flowering shoots which will distribute seed each year. Thus, while larger clones produce many flowering shoots, there are always vegetative shoots and short rhizomes

present to carry on the genet in autumn after flowering shoots die.

SUMMARY AND CONCLUSIONS

Carex comosa shoots may live for up to 700 days, those emerging in autumn usually being longer-lived than shoots emerging in spring and summer. Shoots that emerge in summer and early autumn will develop flower initials during autumn and flower the next June. These flowering shoots also develop axillary shoots during late autumn and early spring which grow and provide a population of young vegetative shoots during the summer. These emergence and growth patterns ensure that mature clones are always a mixture of flowering and vegetative shoots, the former for producing seed to be disseminated to new sites, the latter to provide the clone with a young shoot population after death of the flowering shoots in August. This is important because *C. comosa* acts as a fugitive species, only occupying a site for a certain time so seed production is essential to its establishment in new disturbed sites (Bernard and Fiala, 1986). Other species which grow by both long and short rhizomes may dominate an area; they tend to flower much less and instead reproduce mostly by vegetative means.

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J. M. B.
DEPARTMENT OF BIOLOGY
ITHACA COLLEGE
ITHACA, NY 14850

F. K. S.
DEPARTMENT OF BIOLOGY
ROCHESTER INSTITUTE OF TECHNOLOGY
ROCHESTER, NY 14623

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A COMPUTER METHOD FOR PRODUCING DOT DISTRIBUTION MAPS

RAY ANGELO

ABSTRACT

A method of producing dot distribution maps automatically from a database file using widely available computer software and public domain mapping software is described. Two sample maps are provided.

Key words: atlas, distribution map, MicroCAM, New England, WordPerfect 6.0

While preparing the first installment of an atlas of the vascular plants of New England, a method was developed using various computer software programs to produce dot distribution maps automatically from a database file. This note described the methodology in general terms (but with references to specific software programs) and provides two sample distribution maps produced with this method. More technical details will appear in the first installment of the New England atlas of vascular plants, which is in preparation.

Three computer software programs were used. The mapping software used to produce a customized map of New England with county borders was MicroCAM (Version 3.1). This software, which is for computers that use MS-DOS (most versions), was developed by Dr. Scott A. Loomer (now a professor of geography at the U.S. Military Academy at West Point). Since it is an adaptation of a federally funded mainframe mapping program (CAM), it is in the public domain. It may be obtained at nominal cost from:

Microcomputer Specialty Group of the Assoc.
of American Geographers
% Department of Geography
Indiana University of Pennsylvania
Indiana, PA 15705-1087

The MicroCAM software includes maps of countries, U.S. states, county boundaries, Canadian provinces, coastlines, major rivers, major lakes and major islands derived from World Data Bank II and U.S. Census Bureau boundary files.

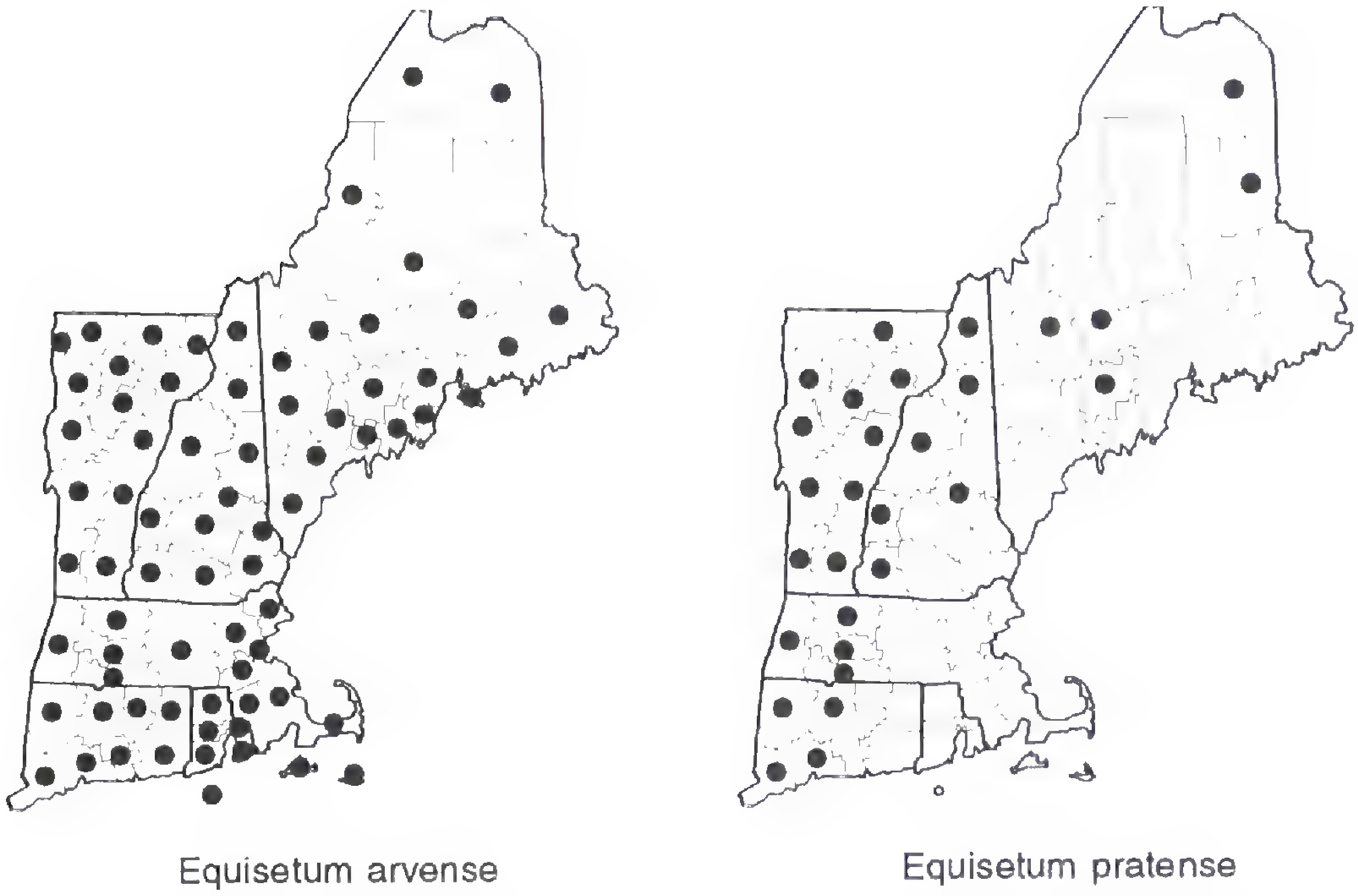

Figure 1. Sample distribution maps produced using the method of this note.

The maps created with MicroCAM can be saved in files in a variety of formats. One of these is Hewlett-Packard Language (HPGL), a standard vector graphics format. The HPGL map files can be imported into WordPerfect 6.0 image files which can then be manipulated. Maps from other mapping programs that can be imported into WordPerfect 6.0 can also be used in this method.

The database software used was Paradox (version 4.0 for DOS) produced by Borland International, Inc. However, any database software that can export its files into ASCII delimited text files (or files of other formats that will be recognized by WordPerfect 6.0 as data files) can be used.

The word processing software WordPerfect 6.0 (product of WordPerfect Corporation) is probably the most vital element of the method. Its ability to manipulate graphics images inside graphics boxes (rectangular areas embedded in a page of text) and its flexibility in allowing the printing of superimposed graphics boxes are critical to the viability of this method. Also, the availability of a scalable, sharp dot in the WordPerfect character sets and a Hewlett-Packard laserjet printer are important. Dots (circular disks) printed by dot matrix printers do not have perfectly circular margins. Similarly, dots produced by some graphics soft-

ware (MicroCAM, for example) are actually many-sided polygons and can be recognized as such.

The basic idea of the method is to perform a merge between a database file containing distribution records and a form file consisting of superimposed graphics boxes. One graphics box contains the outline map (hereafter called a map box). Two other graphic boxes, superimposed over the map box, place dots at specific locations within the box (hereafter called a dot box), depending on the contents of the database fields. A merge is the process that businesses use to produce individualized letters from a customer list (database file) and a form letter (form file).

For the atlas, each taxon is a record in the database file. Each record consists of fields for each component of the scientific name and for each county in New England. Additional fields are provided for the arbitrary subdivisions of some larger counties and for Mt. Desert, Maine and Block Island, Rhode Island. If a herbarium record exists for the taxon in a given county, a letter code for the particular herbarium appears in the field for the county. Otherwise, the given county field is empty. Most of the herbarium records (perhaps 85% to 90%) in the database file are based upon specimens in the New England Botanical Club herbarium.

A map of New England was created using MicroCAM and saved in a file in HPGL format. Then a graphics box (the map box) was designed in WordPerfect 6.0 with the New England map file named as the contents. The image was rotated, shifted and scaled to fit neatly in the graphics box using the image editing capabilities of WordPerfect 6.0. This map box was then saved as a file.

A WordPerfect macro was then created for each New England county. A macro is a sequence of keystrokes that can be executed by pressing one (or a few) preassigned key(s). Each macro created for this method places a dot of a given size at a specific position inside a graphics box (dot box) which is the same size as the map box. The position of the dot is chosen to correspond to the position of the given county in the map box when the dot box is superimposed over the map box. The advantage of defining the macros with respect to the margins of the dot box is that the box may be placed at any position on a page (along with the associated map box) without the need to create a new set of macros.

The form file consists of at least one set of three superimposed graphics boxes. The lowermost is the map box. The next box above (a dot box) contains a set of merge commands that execute

the macros for the counties in Maine, New Hampshire and Vermont for each corresponding nonempty county field in the database file. The uppermost box (a dot box) contains a set of merge commands for the counties in Massachusetts, Rhode Island and Connecticut and a set that produces a caption (the name of the taxon). Two dot boxes were required to hold the merge commands for the counties of New England since one graphics box (of the size used) would not accept the entire set of merge commands. Also, the contents of a graphics box in WordPerfect 6.0 must either be a graphics image or text. There is limited ability to add text to a graphics box containing a graphics image. Since the dots are considered text, it was not possible to place the required merge commands directly into the map box.

Figure 1 is an example of two distribution maps produced using this method with actual data for *Equisetum pratense* Ehrhart and *Equisetum arvense* L. The map was created and imported into WordPerfect 6.0 on a Dell 386 notebook computer. The merge was executed on a Dell 386 desktop computer. The printer used was a Hewlett-Packard Laserjet 4.

This author is unaware of any single, inexpensive software package that accomplishes the results of the method described here. A sophisticated Geographic Information System (GIS) type of software package, PC Arc/Info, made by Environmental Systems Research Institute, no doubt can accomplish the results of this method (except possibly the sharp dots), but its capabilities far exceed what is necessary. Other software programs for IBM compatible computers that might be capable of achieving the results of the method described here are Atlas GIS (Strategic Mapping Inc.), GIS Plus (Caliper Corp.), and MapInfo (MapInfo Corp.). These packages (including PC Arc/Info) are somewhat expensive. Readers interested in geographic data systems for plants should consult the electronic article, "Design Criteria for a Plant Geographic Information System" by Jim Sullivan published in "Flora Online" (Issue #18, Sept. 13, 1988, Text file 018GIS10.TXT, 53,805 bytes), an electronic publication of TAXACOM.

My coworker on the atlas project is David E. Boufford of the Harvard University Herbaria, who I thank for suggestions that improved the wording of this article, for aiding my access to a computer and printer at the Harvard University Herbaria, and for providing a copy of the electronic article referred to in the preceding paragraph.

CURATOR OF VASCULAR PLANTS
NEW ENGLAND BOTANICAL CLUB
HARVARD UNIVERSITY HERBARIA
22 DIVINITY AVE.
CAMBRIDGE, MA 02138

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ADDITIONS TO THE FLORA OF NEWFOUNDLAND. III.

STUART G. HAY, ANDRÉ BOUCHARD, AND LUC BROUILLET

ABSTRACT

Five significant additions of arctic and subarctic species have been made to the native vascular flora of the island of Newfoundland as a result of botanical explorations on the Great Northern Peninsula: *Minuartia biflora* (Wats.) Schinzl. & Thell., *Primula stricta* Hornem., *Sagina caespitosa* (J. Vahl) Lange, *Sagina saginoides* (L.) Karst. and *Salix argyrocarpa* Anderss. Important range extensions on the island are also reported for *Cerastium terrae-novae* Fern. & Wieg., *Danthonia intermedia* Vasey and *Salix arctica* Pallas.

Key Words: vascular flora, arctic and subarctic additions, Newfoundland

Studies on the flora of the island of Newfoundland have taken an important turn recently with the publication of a repertoire with distribution maps of the "Rare Vascular Plants of the Island of Newfoundland" (Bouchard et al., 1991), and a general "Atlas of the Vascular Plants of Newfoundland and the Islands of Saint-Pierre-et-Miquelon" (Rouleau and Lamoureux, 1992). Knowledge of the flora of this insular region of Atlantic Canada continues to progress, but as both of these publications point out, there is still room for work to be done to gain a fuller understanding of the region.

We have already made evident in earlier papers on new records to the flora of Newfoundland (Hay et al., 1990, 1992) that many parts of the island are relatively inaccessible, and have yet to be thoroughly surveyed botanically. Further exploration of these areas is bound to result in exciting new discoveries, range extensions, and to fill in gaps in the presently-known distribution patterns of plants on the island.

In 1992, we pursued our floristic investigations of Newfoundland, particularly of the rare plants, in two areas located at the tip of the Great Northern Peninsula. This area is already known for its important arctic-alpine flora, much of which is rare because of its very restricted distribution on the island. During our field investigations, five remarkable arctic or subarctic species were collected for the first time in Newfoundland. This report includes notes on their distributional range, their habitat, and the phyto-

geographical significance of the new records. All five species make significant additions to both the list of rare plants of Newfoundland (Bouchard et al., 1991) and the recent atlas of the flora of Newfoundland (Rouleau and Lamoureux, 1992).

L'Anse-aux-Meadows

Two species new to Newfoundland were discovered in L'Anse-aux-Meadows National Historic Park, on Sacred Bay, where we conducted a survey of the rare vascular plants for Parks Canada (Bouchard et al., 1993). The park is classified as a World Heritage Site by UNESCO because of its cultural significance as the earliest known Norse landing and settlement site in the New World.

Primula stricta Hornem.

SPECIMENS. **Strait of Belle Isle Dist.**: L'Anse-aux-Meadows National Historic Park, between Upper Quarter Deck Cove and Rudder Cove, 1992/08/08, *Bouchard, Hay & Brouillet 92018* (CAN, COCO, MT).

The distribution of *Primula stricta* extends throughout the southern islands of the Canadian Arctic Archipelago, into the Hudson Bay region and along parts of coastal Ungava and northern Labrador. It is an arctic amphi-Atlantic species that ranges eastward through Greenland and Iceland to Scandinavia (Hultén, 1958; Kelso, 1991). Confusion with other allied species in section *Aleuritia,* namely *Primula anvilensis* S. Kelso, *P. borealis* Duby and *P. incana* M. E. Jones, have, until recently, obscured the true distribution of this species (Kelso, 1991). The only reports of it from Labrador are restricted to the northern coastal area of the Peninsula (Morisset and Payette, 1987; Kelso, pers. comm.).

At the L'Anse-aux-Meadows site, plants of *Primula stricta* were discovered in an open, partly herbaceous Empetrum health community that covered a flat, supralittoral, gravel terrace behind the landwash along a seashore beach. This appears to be typical of the habitat generally observed for the species throughout its range. The plants were past anthesis when collected and were mistaken for efarinose specimens (f. *chlorophylla* Fern.) of *Primula laurentiana* Fern. These two species can be confused, especially where their ranges overlap. No field information was recorded on the size of the colony.

The L'Anse-aux-Meadows record of *Primula stricta* is an important extension southward of the species' range along the Atlantic coast, in comparison with localities in northern Labrador. The origin of the present-day, amphi-Atlantic distribution pattern is still unclear. *P. stricta* is a 14-ploid species that could have derived from either European or North American progenitors. The polyploid complex stems from the postglacial migration and concatenation of ancestral populations following Pleistocene glaciation (Kelso, 1991).

Salix argyrocarpa Anderss. (Syn.: *S. ambigua* Tuckerm., *S. labradorica* Schw.)

SPECIMENS. **Strait of Belle Isle Dist.**: L'Anse-aux-Meadows National Historic Park, along boardwalk between interpretive center and Norse archaeological site, 1992/08/07, *Bouchard, Hay & Brouillet 92001* (CAN, GH, MT)

Endemic to northeastern North America, the range of *Salix argyrocarpa* lies mainly in the northern subarctic regions of the Québec-Labrador Peninsula, with only a few, more southerly localities extending from the eastern James Bay coast to the Côte-Nord of the Gulf of St. Lawrence (Morisset and Payette, 1987; Raup, 1943). Rare and disjunct occurrences appear southward in alpine and subalpine situations in the Shickshock Mountains of the Gaspé Peninsula in Québec and in the New England states of Maine (Mt. Katahdin) and New Hampshire (Mt. Washington) (Crow, 1982; Raup, 1943).

At L'Anse-aux-Meadows, a single colony of this willow was discovered growing in an alder-willow thicket in a zone of heavy snow accumulation. The scrub community was found on sloping, soggy ground below a low, northeast-facing cliff in the bedrock. Less than ten clones were counted in the population.

The Newfoundland population of *Salix argyrocarpa* marks the eastern limit of the species' compass. Although the type of snowbed habitat where it was found may be ecologically restrictive, it seems surprising that this willow has never been recorded on the island. With further search, we would expect it to be found elsewhere in suitable alpine and subalpine sites in the Long Range Mountains and at the tip of the Northern Peninsula.

White Hills Mountains

Three species new to Newfoundland, all Caryophyllaceae, have been discovered in the White Hills Mountains to the west of St. Anthony. The White Hills form two adjoining plateau-like massifs of ultramafic, serpentinized peridotite and dunite bedrock that lie close to the north shore of Hare Bay. The eastern massif forms a high, barren tableland (alt. 230–300 m) covering a vast area of approximately 100 km^2. The northern and eastern rims of the plateau are flanked by steep talus slopes that fall away into a chain of long lakes, two of the largest of which are Eastern Long Pond and Western Long Pond. Snowbeds, some of which are late-lying, are a conspicuous feature of these talus slopes.

The White Hills are of the same geological origin as the serpentine complex in the Bay of Islands and Bonne Bay areas that lie approximately 250 km further south on the west coast. The latter tablelands are already well known for their unique serpentine flora that includes some of the rare and more interesting arctic-alpine and endemic elements of Newfoundland (Bouchard et al., 1986, 1991; Dearden, 1979; Roberts, 1992). The White Hills on the Great Northern Peninsula, however, have been less well explored. Three species, *Cerastium terrae-novae* Fern. & Wieg., *Danthonia intermedia* Vasey and *Salix arctica* Pallas, previously known only from the Bay of Islands and Bonne Bay serpentines, were collected here for the first time, and make significant range extensions on the island.

The three Caryophyllaceae new to Newfoundland are:

Minuartia biflora (Wats.) Schinzl. & Thell. (Syn.: *Arenaria sajanensis* Willd. ex Schlecht., *A. biflora* Wats., not L.)

SPECIMENS. **Strait of Belle Isle Distr.**: White Hills, west of St. Anthony, southwest of Western Long Pond, 1992/08/17, *Bouchard, Hay & Brouillet 92386* (CAN, MT).

Minuartia biflora is a circumpolar, arctic-montane species. In North America, in the western half of its range, it extends from the lower islands of the Canadian Arctic Archipelago southward through Alaska, Yukon and the Rocky Mountains of British Columbia to Colorado and Montana. In the eastern half of its range, *M. biflora* is found from the high Arctic to the Hudson Bay region, and is scattered through the arctic and subarctic region of the

Québec-Labrador Peninsula (Morisset and Payette, 1987; Hultén and Fries, 1986). Only one southward disjunct locality has been recorded from the serpentine summit of Mt. Albert on the Gaspé Peninsula.

On the Eastern White Hills, *Minuartia biflora* was discovered at a single site on the eastern rim of the tableland barrens. Only a few plants were found on patches of exposed, moist gravel on an east-facing slope above a small ravine with late-melting snow. Surprisingly, we did not encounter *M. marcescens* (Fern.) House, the rare, northeastern endemic species that is well known from the Bonne Bay and Bay of Islands serpentines.

The new record on the Great Northern Peninsula for this arctic-alpine species adds a second major, disjunct, southern outpost to the one already known on Mt. Albert in the Shickshock Mountains of the Gaspé. The historical reasons why rare vascular plants and bryophytes with arctic-alpine or Cordilleran affinities have become isolated from their main distribution areas have long been the subject of opposing theories by phytogeographers and ecologists. The question as to whether these plants survived the last glaciation as relicts in *in situ*, ice-free refugia (nunataks) around the Gulf of St. Lawrence, or whether they are post-glacial immigrants from southern or coastal refugia following ice retreat, that subsequently persisted in these unique habitats, is still open to debate (Belland et al., 1992; Bouchard et al., 1986). Their survival in narrow-niche habitats, such as these serpentine barrens, can be attributed to the extreme ecological conditions that tend to reduce competition, favoring the persistance of rare and endemic species at their range limits. Long-distance dispersal is also a possible mechanism that may explain the disjunct distribution pattern of some species.

Sagina caespitosa (J. Vahl) Lange (Syn.: *Sagina nivalis* (Lindbl.) Fries var. *caespitosa* (J. Vahl) Boivin)

SPECIMENS. **Strait of Belle Isle Dist.**: St. Anthony, 4–5 mi. west of town, Eastern White Hills, 1951/06/29, *Savile & Vaillancourt 1971* (MT); 1951/08/08, *Savile & Vaillancourt* (MT).

Sagina caespitosa has a typical arctic amphi-Atlantic distribution pattern. It occurs as a coastal and montane species in the eastern Arctic of North America, radiating eastward across the Atlantic through Greenland, Iceland and Scandinavia (Crow, 1978;

Hultén, 1958; Scoggan, 1978–79). In the arctic region of the Québec-Labrador Peninsula, populations are widespread but rare (Bouchard et al., 1983; Morisset and Payette, 1987; Rousseau, 1974).

The discovery of this remarkable new *Sagina* for Newfoundland results from our revision of older herbarium sheets of collections made in 1951 from the Eastern White Hills tableland, erroneously identified as *Minuartia rubella* (Wahlenb.) Hiern. These Savile and Vaillancourt collections have only recently been made available for consultation and have escaped revision until now. The label information on the herbarium specimens gives only a vague description of the habitat as serpentine gravel barrens at 200 m alt. At the time of our foray on the tableland, we were as yet unaware of the existence of these older specimens, and we did not discover it ourselves during our own collecting.

The new record from the tip of the Northern Peninsula represents a major disjunct outlier to the south. Crow (1978) has discussed the present-day distribution patterns of the different species of *Sagina* in context of Pleistocene glaciation events. He has argued that eastern Arctic populations of *S. caespitosa* may have survived in coastal mountain refugia and cites as evidence their distinct affinity with probable nunatak populations of this species in western Greenland. He is, nonetheless, careful to point out that long distance, airborne dispersal may have played an important role, allowing species of *Sagina,* because of their dust-like diaspores, to become established in suitable habitats following glaciation.

Sagina saginoides (L.) Karst. (Syn.: *Sagina linnaei* Presl)

SPECIMENS. **Strait of Belle Isle Distr**.: White Hills, west of St. Anthony, southwest of Western Long Pond, 1992/08/17, *Bouchard, Hay & Brouillet 92349* (CAN, MT).

Sagina saginoides has a circumpolar distribution, correlating almost entirely with montane regions of the Northern Hemisphere. In North America, it is almost exclusively a western alpine species, ranging through the Cordillera from Alaska south to Arizona and New Mexico (Crow, 1978; Hultén and Fries, 1986). It is of rare occurrence in eastern North America, where only seven disjunct locations have been previously recorded from the arctic

and subarctic region of the Québec-Labrador Peninsula and on the Gaspé Peninsula serpentines of Mt. Albert (Bouchard et al., 1983; Crow, 1978; Morisset and Payette, 1987; Scoggan, 1978–79).

On the Eastern White Hills serpentine plateau, *Sagina saginoides* was discovered along the eastern rim of the tableland where several of the talus slopes are snow-covered until late in the season. Snowbed ecosystems have a particularly high incidence of rare plants in Newfoundland (Bouchard et al., 1991). Their special ecological conditions account for the presence of this new species and other rare, characteristic elements of arctic-alpine affinity such as *Cassiope hypnoides* (L.) D. Don, *Epilobium anagallidifolium* Lam., *E. lactiflorum*Hausskn., *Gnaphalium norvegicum* Gunn., *Phleum alpinum* L., *Salix herbacea* L., *Veronica wormskjoldii* Roem. & Schultes, and *Viola palustris* L. The populations of *Cassiope hypnoides, Salix herbacea* and *Viola palustris* are new records for the area, being formerly known only from more southern alpine summits in the Long Range Mountains, between the Bay of Islands and the Highlands of Saint John (Bouchard et al., 1991).

Sagina saginoides was one of the arctic-alpine species that Fernald (1925) cited as evidence of a disjunct relictual flora that may have survived glaciation in ice-free, nunatak refugia, such as the summit of Mt. Albert on the Gaspé. More recently, however, Crow (1978) has reexamined the phytogeography of this species, and he feels that, in light of today's evidence, the rare and widely isolated eastern populations in Québec and Labrador are better regarded as resulting from long distance dispersal and/or of a pleistocene fragmentation of what was once a more wide-ranging arctic-circumpolar distribution.

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Funding for the study of the rare plants of L'Anse-aux-Meadows National Historic Park came from Parks Canada, Ottawa. G. Argus (Canadian Museum of Nature, Ottawa) kindly identified specimens of *Salix*. G. Crow (University of New Hampshire, Durham) confirmed our identifications of *Sagina* and *Minuartia*. *Primula* specimens were revised by S. Kelso (Colorado College, Colorado Springs).

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INSTITUT DE RECHERCHE EN BIOLOGIE VÉGÉTALE
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A COMPARISON OF THE MARINE ALGAE FROM THE GOLETA SLOUGH AND ADJACENT OPEN COAST OF GOLETA/SANTA BARBARA, CALIFORNIA WITH THOSE IN THE SOUTHERN GULF OF MAINE[1]

ARTHUR C. MATHIESON AND EDWARD J. HEHRE

ABSTRACT

The seaweed floras from the Goleta Slough and adjacent coastal sites near Santa Barbara, California are compared with several coastal and estuarine habitats within the southern Gulf of Maine. One hundred fifty-two taxa are described from the Goleta-Santa Barbara area, consisting of 104 Rhodophyta, 22 Phaeophyta and 26 Chlorophyta. Four of these taxa represent modest range extensions within the state (i.e., *Farlowia conferta, Giffordia hincksiae* var. *californica, Lomentaria caseae* and *Prionitis australis,* while two others found within the Slough (*Capsosiphon fulvescens* and *Microspora pachyderma*) are significant additions to the marine flora of the Pacific Coast. The patterns of species richness and composition at four contiguous southern California sites showed strong contrasts due to local environmental variability, with the highest numbers of taxa (117 taxa or ~77%) occurring at the sand-abraded nearshore Goleta Point site and the lowest within the shallow Slough (26 taxa or ~17%). The depauperate flora of this small arid salt marsh habitat is dominated by ephemeral green algae (16 species) and *Salicornia virginica,* with ten other seaweeds (i.e., 7 reds and 3 browns) only occurring just upstream from its mouth. By contrast, estuarine seaweed floras within New England usually have much higher numbers of red algal taxa, their "open coastal" floras often extend much farther inland (~2.0–8.5 miles) and seaweed standing stocks are usually dominated by fucoid brown algae. The similarity of the Slough's green algal flora to New England's estuarine vegetation is striking, with most of the latter sites exhibiting floristic affinities of 50% or more. The analogous distributional and abundance patterns of ephemeral green algae (*Cladophora sericea* and *Enteromorpha compressa*) and the California horn snail (*Cerithidea califor-*

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[1] Scientific Contribution from the New Hampshire Agricultural Experiment Station; also issued as contribution Number 287 from the Jackson Estuarine Laboratory and the Center for Marine Biology.

nica) suggest several important interactions between seaweeds and snails, plus several other invertebrates and birds.

Key Words: seaweeds, estuarine, coastal, Goleta Slough, southern California, New England

INTRODUCTION

Even though the marine flora of California has a long history of investigations (Papenfuss, 1976), there is a lack of information about seaweed communities at individual sites and man's effect on them (Murray, 1974; Murray and Littler, 1989). In southern California, Dawson (1959a, 1959b, 1965) conducted some of the earliest investigations of intertidal seaweeds during 1956–59, providing a "semi-quantitative baseline" of floras at 44 stations between Point Conception and the U.S.-Mexican border. He concluded that a major reduction of species richness had occurred at some sewage-impacted sites within Los Angeles County since the early 1900's, and an increase of selected articulated corallines. After resurveying 15 of Dawson's southern California sites between Point Dume and Dana Point during 1968–70, Widdowson (1971) found a further reduction in species richness. He suggested that sewage discharge, along with foot traffic and air pollution, were important factors causing an abundance of gelidioid turf algae (*Gelidium coulteri/G. pusillum*) and articulated corallines (Thom and Widdowson, 1978). Subsequent to the Santa Barbara oil spill in 1969, several investigators (e.g., Foster et al., 1971; Nicholson and Cimberg, 1971; Straughn, 1971) documented a further loss of some species and an increase of others (e.g., *Ulva, Corallina* and *Gelidium*) which were capable of uptaking dissolved amino acids (Murray, 1974; North et al., 1970). In discussing short-term plant loss immediately after the spill, Foster et al. (loc. cit.) noted a strong interaction between oil dispersal, storms and sand fluctuations. Three and one-half years later, Cimberg et al. (1973) re-investigated several intertidal beaches near Santa Barbara and stated that periodic inundations by sand were more important than oil in altering rocky epibenthic communities (Emerson and Zedler, 1978; Littler, 1980; Littler et al., 1991; Nicholson, 1972; Nicholson and Cimberg, 1971; Stewart, 1983; Thom and Widdowson, 1978; Widdowson, 1971). In ranking the effects of the Santa Barbara oil spill, Nicholson (loc. cit.) commented that is was only one of several abuses to these coastal

waters, many of which dated back to the 1920's. In summarizing the effects of chronic long-term pollution near a natural oil seep in Goleta (i.e., Coal Oil or Devereaux Point), Littler et al. (1991) stated that several seaweeds either failed to recruit or recolonized very slowly, while Foster et al. (1971) and Nicholson and Cimberg (1971) noted diminutive and/or depauperate floras. In comparing the ecology of a sewage polluted site on San Clemente Island, Murray and Littler (1974) found pronounced changes in species richness and reduced spatial heterogeneity versus nearby controls.

Until recently, estuaries have been the least studied coastal environments in California (Josselyn, 1983; Macdonald, 1977; Macdonald and Barbour, 1974; Zedler, 1982b; Zedler and Nordby, 1986). In addition, most studies of estuarine seaweeds have emphasized productivity and ecological evaluations (Rudnicki, 1986; Shellem and Josselyn, 1982; Zedler, 1977, 1980, 1982a, 1982b), while there have been relatively few detailed assessments of species composition (Josselyn and West, 1985; Norris, 1970; Ripley, 1969; Silva, 1979). Several factors have contributed to the limited knowledge of estuarine seaweeds: (1) the more localized occurrence of estuarine versus rocky and sandy habitats (Chapman, 1977; Littler et al., 1991; Macdonald, 1977; Onuf, 1987; Reimold, 1977); (2) the muddy and often eutrophied conditions within estuaries versus the clean sand and pounding surf of the open coast (Silva, 1979); (3) the apparent dominance of flowering plants (Mason, 1957); (4) the perceived occurrence of a limited and/or cryptic algal flora and; (5) the massive destruction and alterations of such habitats, particularly within southern California (Macdonald, 1977; Zedler, 1982b). In describing the loss of coastal wetlands in southern California, Zedler (loc. cit.) states that there are about thirty wetlands within this geography with a total area of ~5000 ha (12,500 acres). She also emphasizes that this acreage is ~25% of what existed upon the arrival of European man (Speth 1969). In discussing the functional role of estuarine seaweeds, Mann (1972) states that they provide valuable habitats for a myriad of organisms; they also contribute to organic carbon and detrital cycling (Josselyn and Mathieson, 1978, 1980). With increased eutrophication, massive algal blooms may occur within these sheltered habitats (Bach and Josselyn, 1978; Johnson, 1971; McComb et al., 1981; Norton and Mathieson, 1983; Sawyer, 1965; Sewell, 1982; Silva, 1979; Wilce et al., 1982; Wilkinson, 1980).

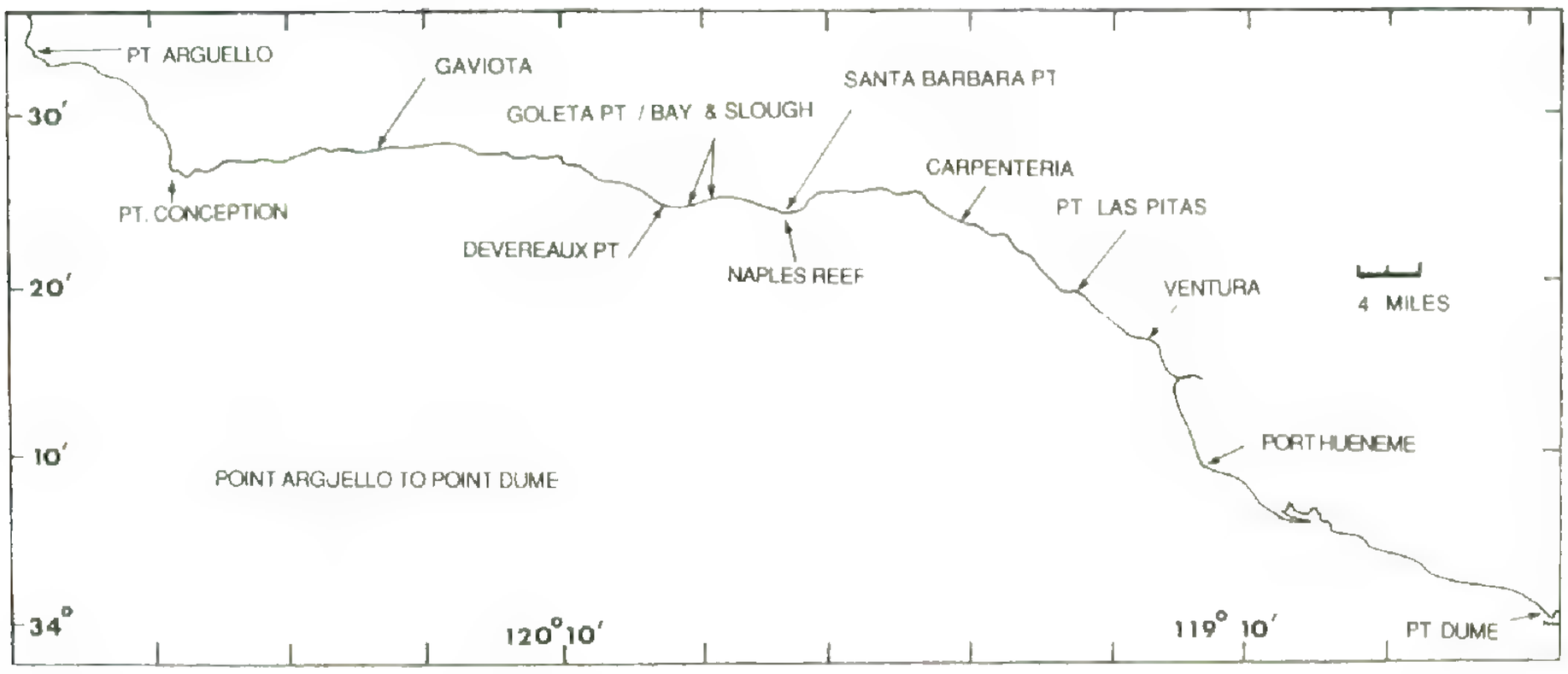


Figure 1. The southern California coastline between Point Arguello and Point Dume, showing the locations of the Goleta Point, Bay and Slough sites, plus Naples Reef.

The present study was initiated to document the open coastal and estuarine seaweeds near Goleta and Santa Barbara, California (Figure 1). We have attempted to summarize the species composition and distributional patterns of marine macrophytes within this arid, Mediterranean geography (Macdonald, 1977; Onuf, 1987; Onuf and Zedler, 1988; Zedler, 1982b; Zedler and Nordby, 1986), comparing them with thirteen New England coastal-estuarine habitats having diverse topographies and hydrographic conditions.

METHODS AND MATERIALS

Seasonal collections and observations of seaweed populations were made during 1979 at four coastal-estuarine habitats between Goleta and Santa Barbara, California (Figure 1 and Appendix). Estuarine collections were made within the Goleta Slough (Figure 2), while open coastal samples were obtained at Goleta Point and within Goleta Bay near the University of California, Santa Barbara Campus (UCSB), as well as at Naples Reef, offshore from Santa Barbara Point. A synopsis of each site's location, general topography and substrata is given in the Appendix. Overall, the most detailed spatial sampling was conducted within the shallow Goleta Slough, while the most comprehensive seasonal collections were made at Goleta Point. Twenty-seven Slough sites were evaluated during the spring and summer, while monthly collections (9 of 12 months) were made along an intertidal-shallow subtidal

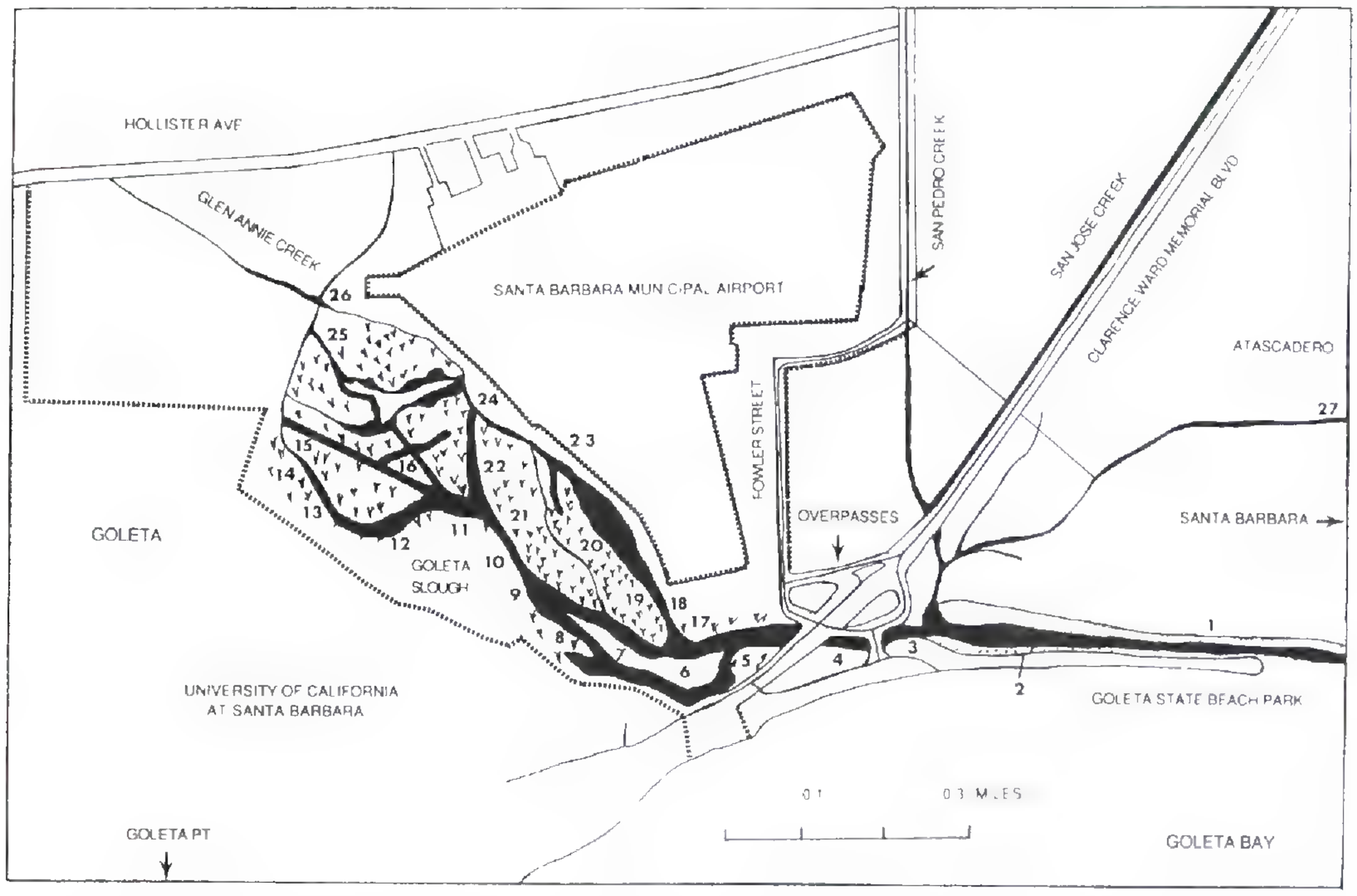


Figure 2. Twenty-seven study sites within the Goleta Slough and the adjacent open coast.

transect at Goleta Point. Periodic subtidal samples (−10 to −30 feet) were made near an experimental farm site in Goleta Bay (Wheeler et al., 1981), while analogous subtidal collections were made at Naples Reef (−15 to −40 feet). All conspicuous seaweeds were collected within the intertidal (on foot) and subtidal zones (by SCUBA) at each site when both habitats were present. The samples were sorted and identified using Abbott and Hollenberg (1976), Scagel et al. (1986) and Stewart (1991) as primary references. Several other synopses were also consulted, including some dealing with North Atlantic seaweeds (e.g., Bliding, 1963, 1968; Collins, 1909, 1912; Dawson, 1946; Scagel, 1966; Silva, 1979; Smith, 1969; South and Tittley, 1986; Sparling, 1971, 1977; Taylor, 1957; Webber and Wilce, 1971; Wilkinson, 1980). Approximately 550 herbarium voucher specimens are deposited in the Albion R. Hodgdon Herbarium (NHA) of the University of New Hampshire to document the region's flora.

A comparison of the number of species in common to the Goleta Slough and thirteen New England estuarine habitats is given, using a variety of published synopses (*see* Mathieson et al., 1993). The nature of these California and New England floras is compared using Cheney's (1977) floristic ratio, (R + C)/P:

$$\frac{\text{\# of Rhodophyta and Chlorophyta species}}{\text{\# of Phaeophyta species}}$$

With this calculation, a value of < 3.0 indicates a temperate or "cold-water" flora, while intermediate values and those > 6.0 indicate "mixed" and "warm-water" floras, respectively. The mean number of taxa/site from the Goleta Slough and thirteen New England estuarine habitats was also compared.

Monthly records of surface water temperatures and salinities were recorded at Goleta Point during 1979, while hydrographic surveys of the Slough were made during the spring and summer of the same year. A hand-held thermometer and refractometer were used for these measurements, having accuracies of 0.1°C and 0.5‰ (i.e., parts per thousand), respectively. Monthly records of sand levels within the intertidal zone at Goleta Point were documented by drawing out a metered line to a uniform distance between two rock outcrops with permanent bench marks (cement nails). Sand levels were determined by plumbing down to the sand/rock interface at ~1.0 m intervals along the transect line (Daly and Mathieson, 1977). All elevations were corrected to mean low water (MLW) after multiple measurements from these bench marks. Monthly comparisons of species richness and sand levels were made.

Abundance patterns of several green algae and the California horn snail, *Cerithidea californica* (Haldeman), were documented from three shallow pans within the Slough. A quadrat frame (1/16 m^2) was positioned at ~0.9 m intervals and the contents sampled. Individual seaweeds were dried (60°C for ~40 hours) and quantified as g dry weight/m^2; snail density was enumerated as #/m^2.

HABITAT DESCRIPTION

As outlined by Ricketts et al. (1985), most of the southern California coastline is exposed to moderate wave action due to an offshore archipelago—the Channel Islands. Even so, a strong gradient of water motion may exist (Wheeler et al., 1981), ranging from Naples Reef (most exposed) to Goleta Point, Bay and Slough (most sheltered). A pronounced gradient of rocky substrata occurs here, with Naples Reef having the most abundant rocky substrata and Goleta Slough the least. The broad sandy beaches at the

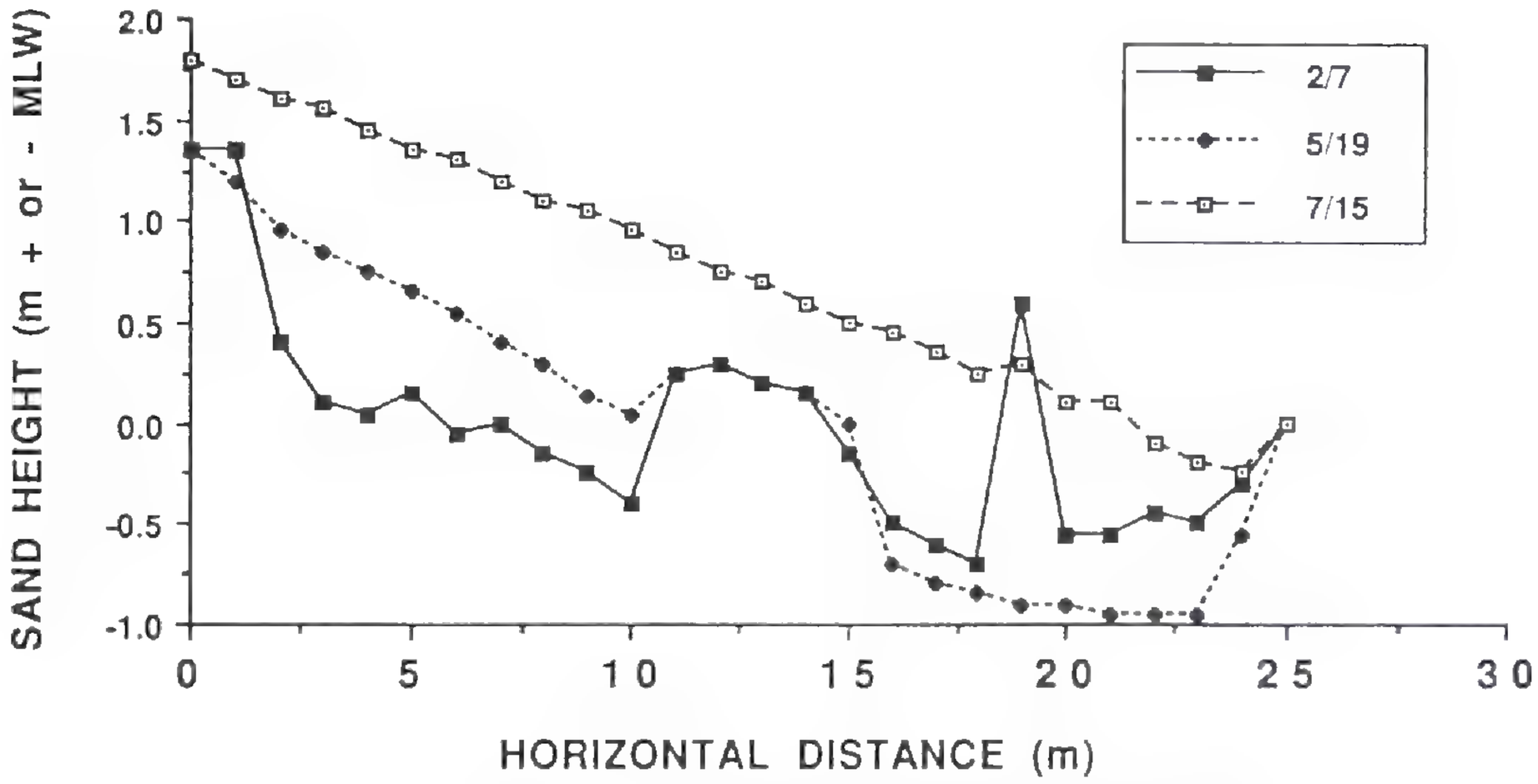


Figure 3. Variation of sand levels at Goleta Point between two major rock outcrops (i.e., at 0 and 10–15 m).

Goleta Point and Bay sites have scattered rock outcrops and boulders (i.e., Monterey shale/siltstone), which are often buried and extensively scoured (Littler et al., 1991). Figure 3 illustrates the variation of sand levels on the Goleta Point transect. Although rather irregular, sand elevations were usually highest during summer (July) and lowest in winter (February). *In situ* organisms growing in such habitats may be removed, scoured or buried by a meter or more of sand during mid-summer.

Goleta Point (Figure 1) is located downstream from a natural oil seep at Coal Oil (Devereaux) Point (Littler et al., 1991). In discussing the effects of the seep, Foster et al. (1971) noted that 30–60% of the rock surfaces at Goleta Point were covered by tar, causing a conspicuous reduction in abundance and stature of benthic organisms. Although we did not quantify the distribution and abundance of this "tar" on the intertidal transect, we concur with Foster et al. (loc. cit.) that it must, at the very least, reduce the availability of rocky substrata for benthic organisms.

Goleta Slough is a small, shallow, arid salt marsh habitat located at ~34°25′N and 119°50′W (Figure 2). As noted by Onuf and Zedler (1988), the average annual precipitation within this locale is < 40 cm (Baldwin, 1974) and the only substantial streamflow occurs just after a major storm. Because of such climatic extremes and the Slough's shallow topography, evaporation usually exceeds precipitation after March and monthly saturation deficits often

exceed 10 cm. Tidal limits of the Slough extend ~1.0–1.2 miles inland from its mouth near Goleta State Beach Park. Like the Tijuana Estuary in San Diego, it is a wetland-dominated habitat, with no major embayment and a relatively narrow ocean connection (Zedler and Nordby, 1986). The Slough is located midway between Santa Barbara's Municipal Airport and the UCSB campus. Thus, it is an urbanized and highly modified estuary (Norris, 1970; Zedler and Nordby, 1986), with its northeastern perimeter drastically altered due to airport expansion, while the construction of overpasses (i.e., for gas pipelines and roads) and bike paths has changed its topography. In addition, a large part of the Slough is in the form of channels, which are artificially deepened for flood control and separated from the adjacent salt marsh by dikes (Onuf, 1987). Currently, the west-central part of the Slough is dominated by three major tidal channels, which bifurcate ~0.52 miles upstream from its mouth near the Clarence Ward Memorial Boulevard overpass. Further upstream (~0.94 miles inland), the source of these tidal channels is evident (i.e., Glen Annie Creek and an unnamed channel running parallel to Aero Camino Road). In the east-central portion of the Slough, three creeks converge between ~0.42–0.51 miles inland, with two originating from S and SW flowing flood channels (i.e., San Pedro and San Jose Creeks, respectively) and one arising from a tributary due east near Atascadero. Twenty-four study sites were established along the west central tidal channels, two near the Slough's mouth and one at the tidal dam near Atascadero (Figure 2 and the Appendix).

Most of the Goleta Slough consists of salt marshes, shallow pans and a series of channels (Appendix). Scattered boulders and artificial structures (i.e., bridge abutments, pilings, broken pieces of asphalt, etc.) are most abundant near the Slough's mouth and occur sporadically upstream. Sand periodically blocks the mouth, restricting tidal exchange and contributing to enhanced summer salinities (Figure 4; Macdonald, 1977; Onuf, 1987; Onuf and Zedler, 1988; Zedler, 1982b). As outlined by Onuf and Zedler (loc. cit.), *Salicornia virginica* L. is the dominant salt marsh plant within this tidally restricted habitat (94% frequency of occurrence), with only patchy amounts (1–2%) of *Cotula coronopifolia* L., *Frankenia grandifolia* Chamiso *et* Schlechtendal and *Lolium perenne* L. Zedler (1982b) lists eleven additional flowering plants from the Slough: *Atriplex watsonii* A. Nelson, *Cressa truxillensis,* H. B. K., *Cuscuta salina* Engelmann, *Distichlis spicata* (L.) Greene,

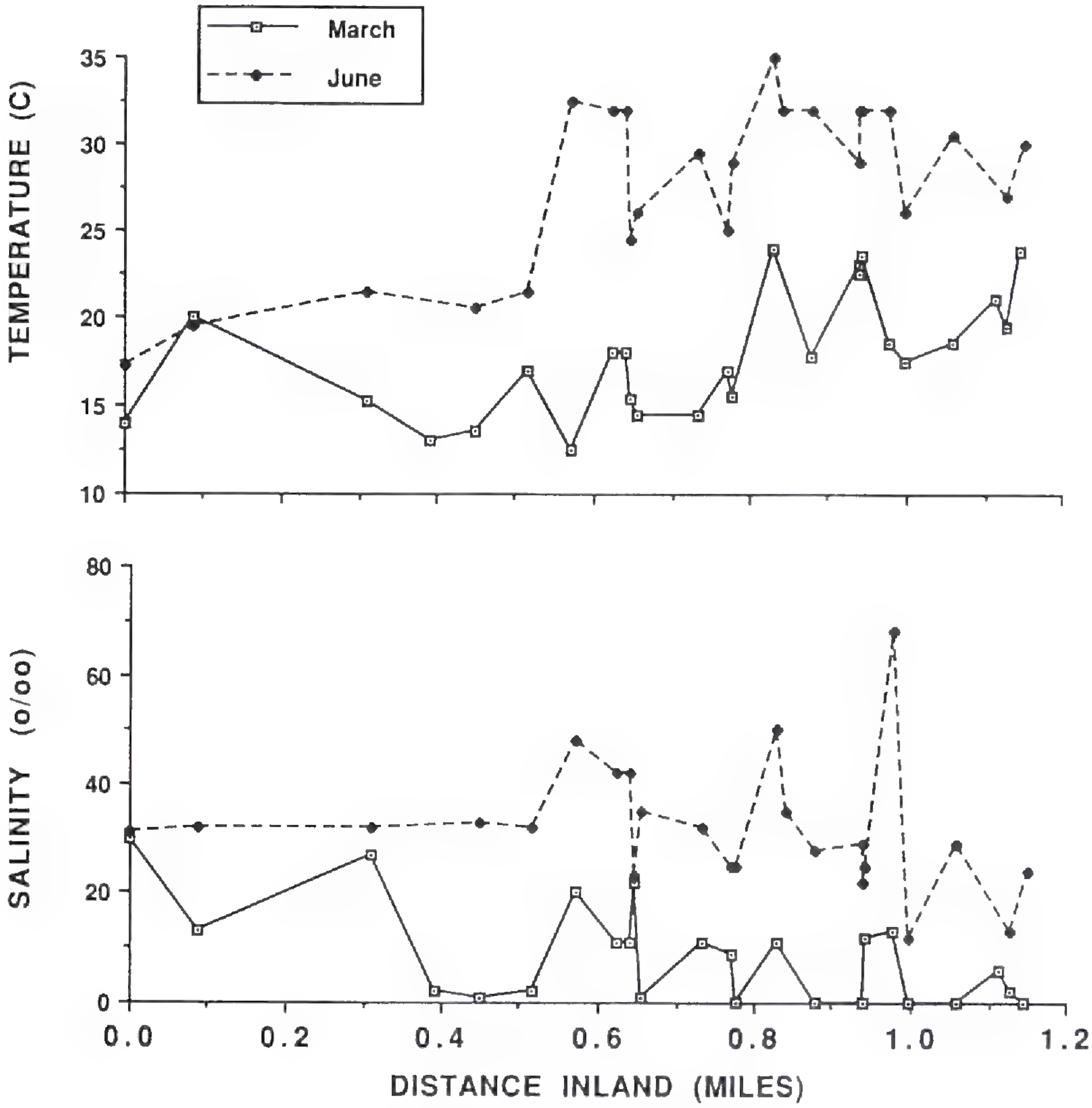


Figure 4. Surface water hydrographic conditions (i.e., temperature and salinity) at Goleta Point and adjacent Slough during March and June of 1979.

Jaumea carnosa (Lessing) Gray, *Lasthenia glabrata* Lindley, *Limonium californicum* Heller, *Monanthochloë littoralis* Engelmann, *Salicornia subterminalis* Parish, *Suaeda californica* Watson and *Triglochin concinnum* Davy. Although we primarily studied the macroalgal communities within the Slough, a variety of *Vaucheria* and microscopic algal mats (i.e., blue-green algae and diatoms) also occur on muddy surfaces (Onuf, 1987; Zedler, 1980, 1982a, 1982b). As outlined by Onuf (loc. cit.), the overall coverage of seaweeds is relatively small versus that of emergent vascular plants. Seaweeds, therefore, grow attached to widely scattered solid substrata, as entangled masses on the banks of tidal channels and as epiphytes upon salt marsh vegetation. The dominant macro-invertebrate within the Slough is *Cerithidea califor-*

nica, the California horn snail (Onuf, 1987; Zedler, 1982b; Zedler and Nordby, 1986).

Figure 4 illustrates surface water temperatures and salinities at Goleta Point and within the Slough during March and June of 1979. Temperatures tended to increase from outer (i.e., site 1) to inner estuarine sites (e.g., 21 and 22), ranging from ~14.0°–24.0°C during March to ~17.0°–35°C in June. Salinities at Goleta Point were relatively constant at 30–31‰, while those within the Slough varied from 0 to ~27 ‰ in March to ~12–68‰ in June. During March, twelve Slough sites had salinities of < 2‰. Three months later (June) the two lowest salinities were 10 and 13‰, while seven sites had salinities > 28‰. A maximum of 68‰ was recorded in one shallow pan with abundant green algae and horn snails (see ABUNDANCE PATTERNS).

SPECIES COMPOSITION AND NEW DISTRIBUTIONAL RECORDS

One hundred fifty-two seaweed taxa were recorded from the four study sites, including 103 Rhodophyceae, 22 Phaeophyceae and 26 Chlorophyceae (Table 1). The highest numbers of taxa or percent contribution to species richness were recorded at Goleta Point (117 taxa or ~77%) and the lowest within the Slough (26 taxa or ~17%). Most taxa from Goleta Point occurred on the shallow transect (i.e., 94 taxa or ~62%), while the remainder were collected immediately offshore from the UCSB campus (i.e., 23 taxa or ~15%). Floristic patterns at Naples Reef and at the offshore Goleta Bay site were somewhat intermediate, with 52 taxa (~34%) occurring at the former and 39 (~26%) at the latter.

The numbers (%) of red, brown and green algal taxa/site were highly variable (Table 1). Green algae were maximal at Goleta Point (19) and within the Slough (16), while the lowest numbers occurred at the offshore Goleta Bay (2) and Naples Reef (1). Brown and red algae were highest at Goleta Point (17 and 81 taxa) and lowest within the Slough (3 and 7 taxa). Green algae dominated the Slough (~62%), were intermediate at Goleta Point (16%) and lowest at the offshore Naples Reef (2%) and Goleta Bay sites (5%). The percentage contribution of brown algae was minimal within the Slough with its depauperate flora (~12%), while it ranged from ~15–33% at the Goleta Point and Bay sites. Red algae dominated at Naples Reef (~85%), were intermediate at the Go-

leta Point and Bay sites (~62–69%) and lowest within the Slough (~27%).

Floristic diversity is further documented using Cheney's (R + C)/P ratio. The highest value was recorded for the Slough (~7.7), followed by the transect (~6.8) and total floras at Goleta Point (~5.9), Naples Reef (~7.7), and Goleta Bay (2.0). Thus, most of the floras would be interpreted as "warm-water," except for the offshore Goleta Bay site.

Six of the 152 taxa recorded here (Table 1) represent new geographical records. Two were collected from Goleta Slough (*Capsosiphon fulvescens* and *Microspora pachyderma*) and four from the open coast (*Farlowia conferta, Giffordia hincksiae* var. *californica, Lomentaria caseae* and *Prionitis australis*). *Capsosiphon fulvescens* was previously known from northern British Columbia and Vancouver Harbor (Garbary et al., 1982), while the only previous "marine" records for the freshwater green algae *M. pachyderma* (Collins, 1909; Prescott, 1962) were from several western North Atlantic estuaries (Mathieson and Hehre, 1986; Mathieson and Penniman, 1986a, 1991; Mathieson et al., 1993). The records of *G. hincksiae* var. *californica, F. conferta* and *P. australis* are modest extensions beyond San Luis Obispo County (i.e., Point Conception), while the occurrence of *Lomentaria caseae* is a northern expansion of its known range from Del Mar within San Diego County to Isla Guadalupe, Baja California (Abbott and Hollenberg, 1976; Scagel et al., 1986; Stewart, 1991).

DISTRIBUTIONAL PATTERNS AND FLORISTIC COMPARISONS

Seaweeds at the four study sites exhibited three local distributional patterns (Figure 5 and Table 1):

(1) Coastal—restricted to the nearshore open coast (126 taxa or ~83%).
(2) Cosmopolitan—present in estuarine and open coastal environments (20 taxa or ~13.0%).
(3) Estuarine—restricted to Goleta Slough (6 taxa or ~4.0%).

All six estuarine seaweeds were green algae, including *Capsosiphon fulvescens, Cladophora microcladioides, Enteromorpha intestinalis, Microspora pachyderma, Rhizoclonium riparium* and *Ulvaria oxysperma*. In contrast, coastal taxa consisted of 97 Rhodophyceae, 19 Phaeophyceae and 10 Chlorophyceae, while the

Table 1. Seaweed taxa from three open coastal sites and one estuarine habitat near Goleta, California.

	1a	1b	2	3	4
Chlorophyta					
Acrochaete viridis (Reinke) R. Nielsen	x	x			
Blidingia minima (Nägeli *ex* Kützing) Kylin	x	x		x	
Bryopsis corticulans Setchell	x	x			
Bryopsis hypnoides Lamouroux	x	x			
Capsosiphon fulvescens (C. Agardh) Setchell *et* Gardner				x	
Chaetomorpha aerea (Dillwyn) Kützing	x	x		x	
Cladophora columbiana Collins	x	x			
Cladophora graminea Collins	x	x			
Cladophora microcladioides Collins				x	
Cladophora sericea (Hudson) Kützing	x	x		x	
Codium sp. (basal filaments)	x	x			
Codium fragile (Suringar) Hariot					x
Enteromorpha clathrata (Roth) Greville	x	x		x	
Enteromorpha compressa (L.) Greville	x	x		x	
Enteromorpha flexuosa (Roth) J. Agardh ssp. *flexuosa*	x	x		x	
Enteromorpha intestinalis (L.) Link				x	
Enteromorpha linza (L.) J. Agardh	x	x	x	x	
Enteromorpha prolifera (Müller) J. Agardh	x	x		x	
Microspora pachyderma (Wille) Lagerheim				x	
Rhizoclonium implexum (Dillwyn) Kützing	x	x			
Rhizoclonium riparium (Roth) Harvey				x	
Ulva californica Wille	x	x			
Ulva costata (Howe) Hollenberg		x			
Ulva lactuca L.	x	x	x	x	

Table 1. Continued.

	1a	1b	2	3	4
Ulva taeniata (Setchell) Setchell *et* Gardner	x	x		x	
Ulvaria oxysperma (Kützing) Bliding				x	
Total green algal taxa/site	18	19	2	16	1
Total green algal taxa (26)	1a	1b	2	3	4
Phaeophyta					
Colpomenia sinuosa (Roth) Derbès *et* Solier	x	x			
Cylindrocarpus rugosus Okamura	x	x			
Cystoseira osmundacea (Turner) C. Agardh		x	x		x
Desmarestia ligulata (Lightfoot) Lamouroux var. *firma* (C. Agardh) J. Agardh					x
Desmarestia ligulata (Lightfoot) Lamouroux va. *ligulata*		x	x		x
Desmarestia viridis (Müller) Lamouroux			x		
Dictyota binghamiae J. Agardh					x
Ectocarpus parvus (Saunders) Hollenberg	x	x	x	x	x
Egregia menziesii (Turner) Areschoug	x	x	x		
Endarachne binghamiae J. Agardh	x	x	x	x	
Giffordia hincksiae (Harvey) Hamel var. *californica* Hollenberg et Abbott			x		
Giffordia sandriana (Zanardini) Hamel	x	x	x		
Haplogloia andersonii (Farlow) Levring			x		
Hincksia granulosa (J. E. Smith) Hamel	x	x	x		
Laminaria farlowii Setchell		x	x		x
Macrocystis pyrifera (L.) C. Agardh		x	x		
Pterygophora californica Ruprecht		x			x

Table 1. Continued.

	1a	1b	2	3	4
Scytosiphon dotyi Wynne	x	x			
Scytosiphon lomentaria (Lyngbye) J. Agardh	x	x	x		
Sphacelaria didichotoma Saunders	x	x			
Taonia lennebackerae J. Agardh	x	x		x	
Zonaria farlowii Setchell *et* Gardner	x	x			
Total brown algal taxa/site	12	17	13	3	7
Total brown algal taxa (22)					
Rhodophyta					
Acrosorium venulosum (Zanardini) Kylin			x		x
Ahnfeltia fastigiata (Postels *et* Ruprecht) Makienko	x	x			
Antithamnion defectum Kylin	x	x			
Asterocolax gardneri (Setchell) Feldmann *et* Feldmann	x	x			
Audouinella daviesii (Dillwyn) Woelkerling	x	x			
Bangia vermicularis Harvey	x	x			
Bossiella orbigniana (Decaisne) Silva ssp. *dichotoma* (Manza) Johansen	x	x			x
Bossiella orbigniana (Decaisne) Silva ssp. *orbigniana*	x	x			x
Botryocladia hancockii Dawson					x
Botryocladia neushulii Dawson		x	x		
Botryocladia pseudodichotoma (Farlow) Kylin					x
Calliarthron cheilosporioides Manza					x
Callithamnion biseriatum Kylin			x		
Callophyllis firma (Kylin) R. Norris					x

Table 1. Continued.

	1a	1b	2	3	4
Callophyllis flabellulata Harvey		x	x		
Callophyllis pinnata Setchell *et* Swezy		x			
Callophyllis violacea J. Agardh		x	x		
Centroceras clavulatum (C. Agardh) Montagne	x	x	x		
Ceramium californicum J. Agardh	x	x			
Ceramium eatonianum (Farlow) DeToni	x	x			
Ceramium sinicola Setchell *et* Gardner	x	x			
Ceramium zacae Setchell *et* Gardner					x
Chondria nidifica Harvey	x	x		x	x
Corallina officinalis L. var. *chilensis* (Decaisne) Kützing	x	x			x
Corallina vancouveriensis Yendo	x	x			
Cryptopleura corallinara (Nott) Gardner	x	x			
Cryptopleura crispa Kylin	x	x			
Cryptopleura ruprechtiana (J. Agardh) Kylin		x			
Cryptopleura violacea (J. Agardh) Kylin	x	x	x		x
Cumagloia andersonii (Farlow) Setchell *et* Gardner	x	x			
Erythrotrichia carnea (Dillwyn) J. Agardh	x	x			
Farlowia conferta (Setchell) Abbott					x
Fryeella gardneri (Setchell) Kylin		x			x
Gastroclonium subarticulum (Turner) Kützing	x	x			
Gelidiocolax microsphaerica Gardner	x	x			
Gelidium coulteri Harvey	x	x		x	
Gelidium purpurascens Gardner		x			
Gelidium pusillum (Stackhouse) Le Jolis	x	x			
Gelidium robustum (Gardner) Hollenberg *et* Abbott		x	x		x

Table 1. Continued.

	1a	1b	2	3	4
Gigartina canaliculata Harvey	x	x	x	x	
Gigartina exasperata Harvey *et* Bailey		x			x
Gigartina harveyana (Kützing) Setchell *et* Gardner			x		
Gigartina leptorhynchos J. Agardh	x	x		x	
Gigartina ornithorhynchos J. Agardh	x	x			
Gigartina volans (C. Agardh) J. Agardh	x	x			
Gracilaria papenfussii Abbott	x	x	x		x
Gracilaria textorii (Suringar) J. Agardh var. *cunninghamii* (Farlow) Dawson	x	x			
Gracilariophila oryzoides Setchell *et* Wilson	x	x			
Grateloupia doryphora (Montagne) Howe	x	x	x		x
Gymnogongrus chiton (Howe) Silva *et* DeCew	x	x	x		x
Gymnogongrus leptophyllus J. Agardh	x	x			
Halymenia californica Smith *et* Hollenberg			x		x
Halymenia hollenbergii Abbott					x
Herposiphonia plumula (J. Agardh) Hollenberg					x
Herposiphonia secunda (C. Agardh) Ambron forma *tenella* (C. Agardh) Wynne	x	x			
Herposiphonia verticillata (Harvey) Kylin	x	x			
Heterosiphonia japonica Yendo					x
Holmesia californica (Dawson) Dawson	x	x			x
Janczewksia lappacea Setchell	x	x			
Laurencia pacifica Kylin	x	x			x
Laurencia spectabilis Postels *et* Ruprecht	x	x			
Lomentaria caseae Dawson					x

Table 1. Continued.

	1a	1b	2	3	4
Mastocarpus papillatus (C. Agardh) Kützing	x	x			
Melobesia marginata Setchell *et* Foslie	x	x			
Melobesia mediocris (Foslie) Setchell *et* Mason	x	x			
Microcladia coulteri Harvey	x	x	x		x
Nemalion helminthoides (Velley) Batters	x	x			
Nienbergia andersoniana (J. Agardh) Kylin	x	x	x		x
Nitophyllum northii Hollenberg *et* Abbott			x		
Opuntiella californica (Farlow) Kylin			x		
Phycodrys isabelliae R. Norris *et* Wynne					x
Platythamnion heteromorphum (J. Agardh) J. Agardh					x
Platythamnion pectinatum Kylin					x
Platythamnion villosum Kylin		x	x		
Pogonophorella californica (J. Agardh) Silva	x	x			
Polyneura latissima (Harvey) Kylin		x	x		x
Polysiphonia hendryi Gardner	x	x		x	x
Polysiphonia pacifica Hollenberg	x	x	x		
Polysiphonia scopulorum Harvey var. *villum* (J. Agardh) Hollenberg	x	x			
Porphyra perforata J. Agardh	x	x			
Prionitis angusta (Harvey) Okamura		x			x
Prionitis australis (J. Agardh) J. Agardh		x			x
Prionitis lanceolata (Harvey) Harvey	x	x			
Pterochondria woodii (Harvey) Hollenberg	x	x			
Pterocladia capillacea (Gmelin) Bornet *et* Thuret		x			
Pterosiphonia baileyi (Harvey) Falkenberg	x	x			

Table 1. Continued.

	1a	1b	2	3	4
Pterosiphonia dendroidea (Montagne) Falkenberg	x	x		x	x
Rhodoglossum affine (Harvey) Kylin	x	x			
Rhodoglossum californicum (J. Agardh) Abbott	x	x			
Rhodoglossum roseum (Kylin) G. M. Smith		x			
Rhodoptilum plumosum (Harvey *et* Bailey) Kylin					x
Rhodymenia arborescens Dawson					x
Rhodymenia californica Kylin var. *attenuata* (Dawson) Dawson					x
Rhodymenia californica Kylin var. *californica*			x		x
Rhodymenia pacifica Kylin	x	x	x		x
Sarcodiotheca furcata (Setchell *et* Gardner) Kylin		x			x
Sarcodiotheca gaudichaudii (Montagne) Gabrielson	x	x	x		x
Scinaia articulata Setchell	x	x			x
Scinaia confusa (Setchell) Huisman	x	x			
Schizmenia pacifica Kylin	x	x			x
Smithora naiadum (Anderson) Hollenberg	x	x			
Stenogramme interrupta (C. Agardh) Montagne	x	x			
Stylonema alsidii (Zanardini) Drew	x	x		x	
?*Tenarea dispar* (Foslie) Adey		x			
Total red algal taxa/site	64	81	24	7	44
Total red algal taxa (104)					
Total taxa/site	94	117	39	26	52
Total taxa (152)					

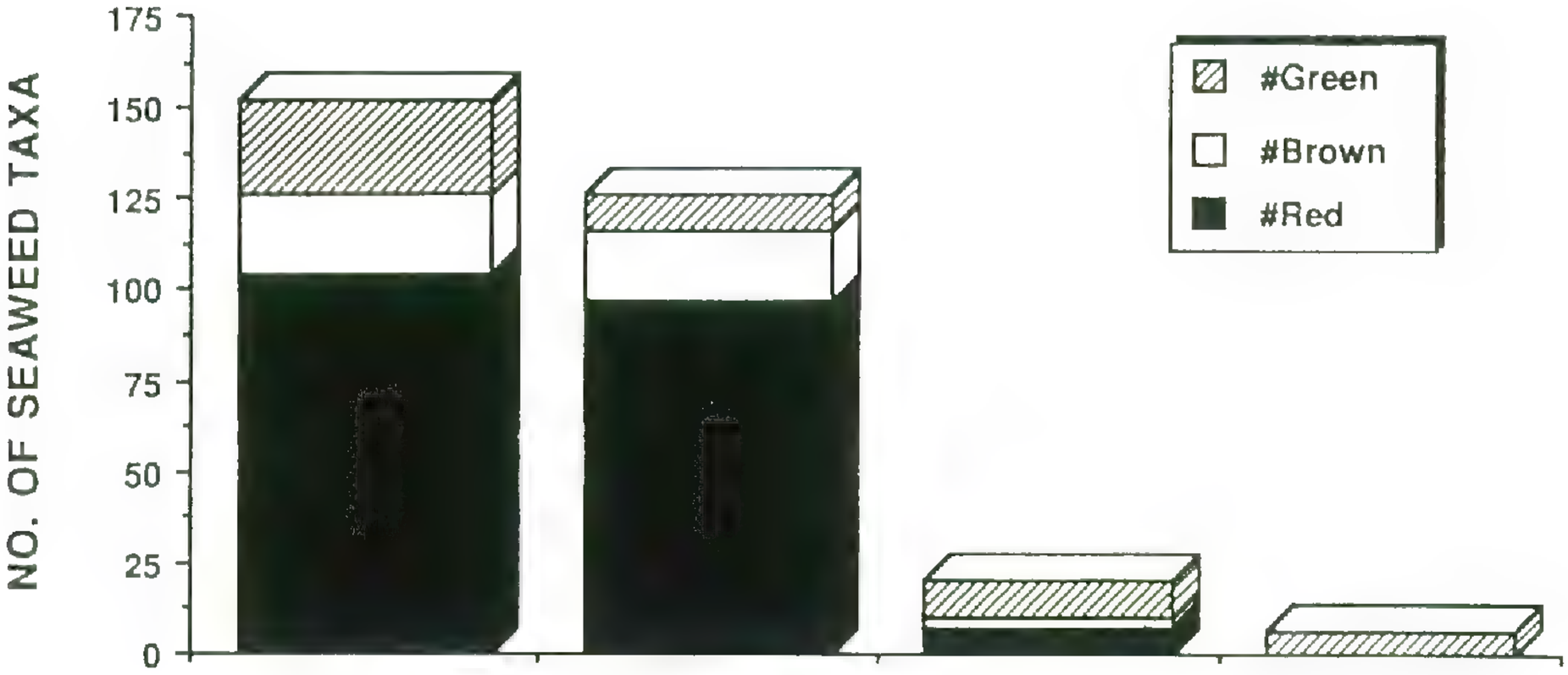
#1a = Goleta Point (transect, intertidal & shallow subtidal); #1b = Goleta Point (total flora, intertidal & subtidal); #2 = Goleta Bay (offshore-subtidal); #3 = Goleta Slough (intertidal & subtidal); #4 = Naples Reef (offshore-subtidal).

cosmopolitan component contained 7 Rhodophyceae, 3 Phaeophyceae and 10 Chlorophyceae. Approximately 31% of the coastal taxa occurred at two or more sites (39 taxa), while the remaining 87 were restricted to one of the following sites: (1) Goleta Point transect—9 Chlorophyceae, 4 Phaeophyceae and 45 Rhodophyceae; (2) Offshore Goleta Point—1 Chlorophyceae and 4 Rhodophyceae; (3) Goleta Bay—3 Phaeophyceae and 4 Rhodophyceae; (4) Naples Reef—1 Chlorophyceae, 2 Phaeophyceae and 17 Rhodophyceae. One cosmopolitan taxa occurred at all four sites (i.e., *Ectocarpus parvus*), while seven were found at three sites (i.e., *Enteromorpha linza, Ulva lactuca, Endarachne binghamiae, Chondria nidifica, Gigartina canaliculata, Polysiphonia hendryi* and *Rhodoglossum affine*). See Table 1 for specific details.

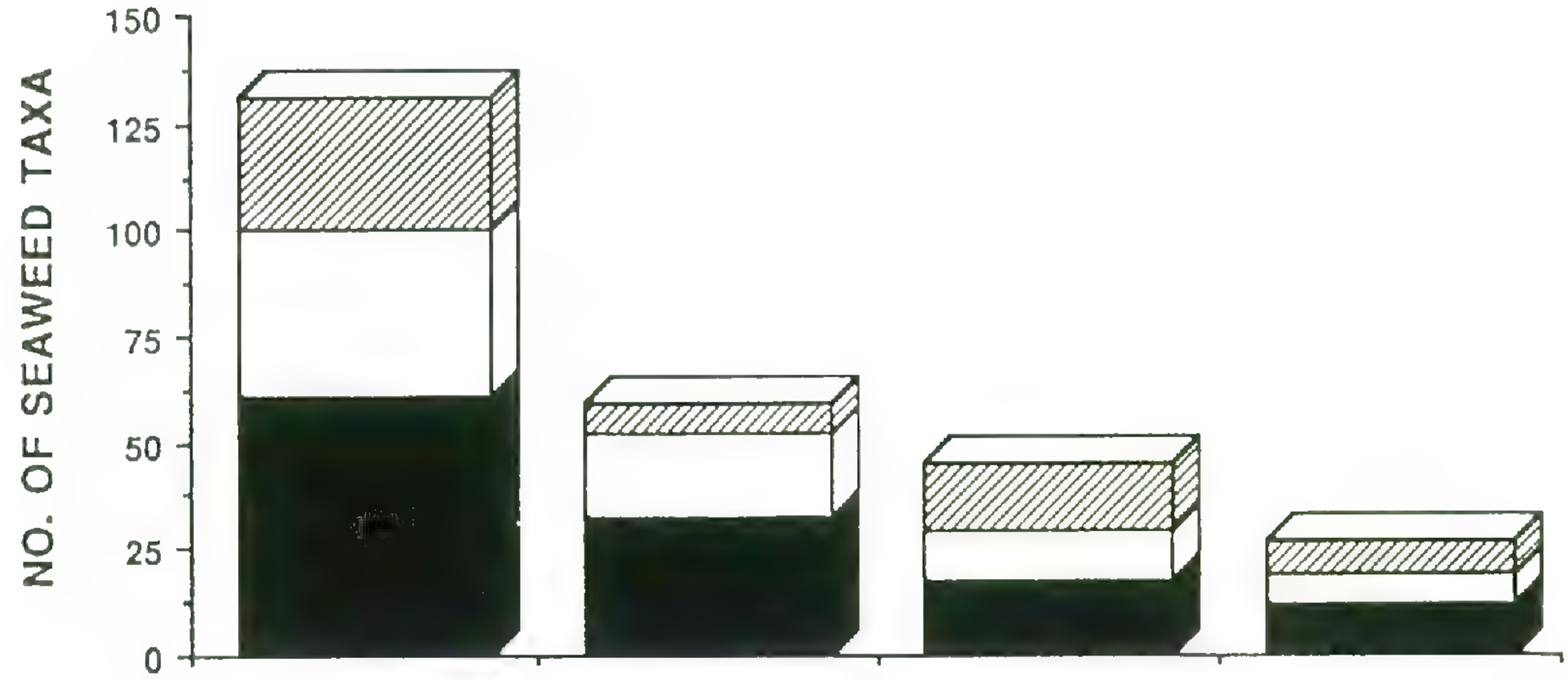
A comparison of the floras from Goleta Slough and the adjacent open coast with two analogous New England habitats (i.e., the York River and Great Bay Estuarine areas) shows varying patterns of local distribution (Figure 5). For example, 131 taxa occur within the York River Estuary and adjacent open coast of southern Maine, consisting of 59 coastal, 45 cosmopolitan and 27 estuarine (Mathieson, et al., 1993). The flora within the Great Bay Estuary and adjacent open coast is more diverse (i.e., 194 taxa), consisting of 21 coastal, 149 cosmopolitan and 24 estuarine taxa (Mathieson and Hehre, 1986). Thus, the estuarine reduction pattern is most conspicuous within Goleta Slough (i.e., 126 coastal, 20 cosmopolitan and 6 estuarine), intermediate within the York River Estuary, and least pronounced within the Great Bay Estuary. Floristic patterns within the Goleta Slough and York River are similar, except for differences in the numbers of total taxa and brown and red algae. The prevalence of cosmopolitan taxa within the Great Bay area (77%) should be emphasized, as it represents a very different pattern than that found within either the York River (34%) or Goleta Slough (13%).

The number of seaweed taxa/site within Goleta Slough is summarized in Figure 6 and Table 2. The highest number of taxa was recorded at site 1 (22), while reduced and irregular numbers occurred upstream (i.e., 1–13). Green algae dominated the Slough, with *Enteromorpha clathrata* and *Rhizoclonium riparium* exhibiting occurrences of 85.2 and 81.5%, respectively. All seven red algae and two of the three browns were restricted to site 1 (i.e., 3.7% occurrence), which is just 0.09 miles inland from the mouth. Only one brown alga (*Ectocarpus parvus*) extended upstream be-

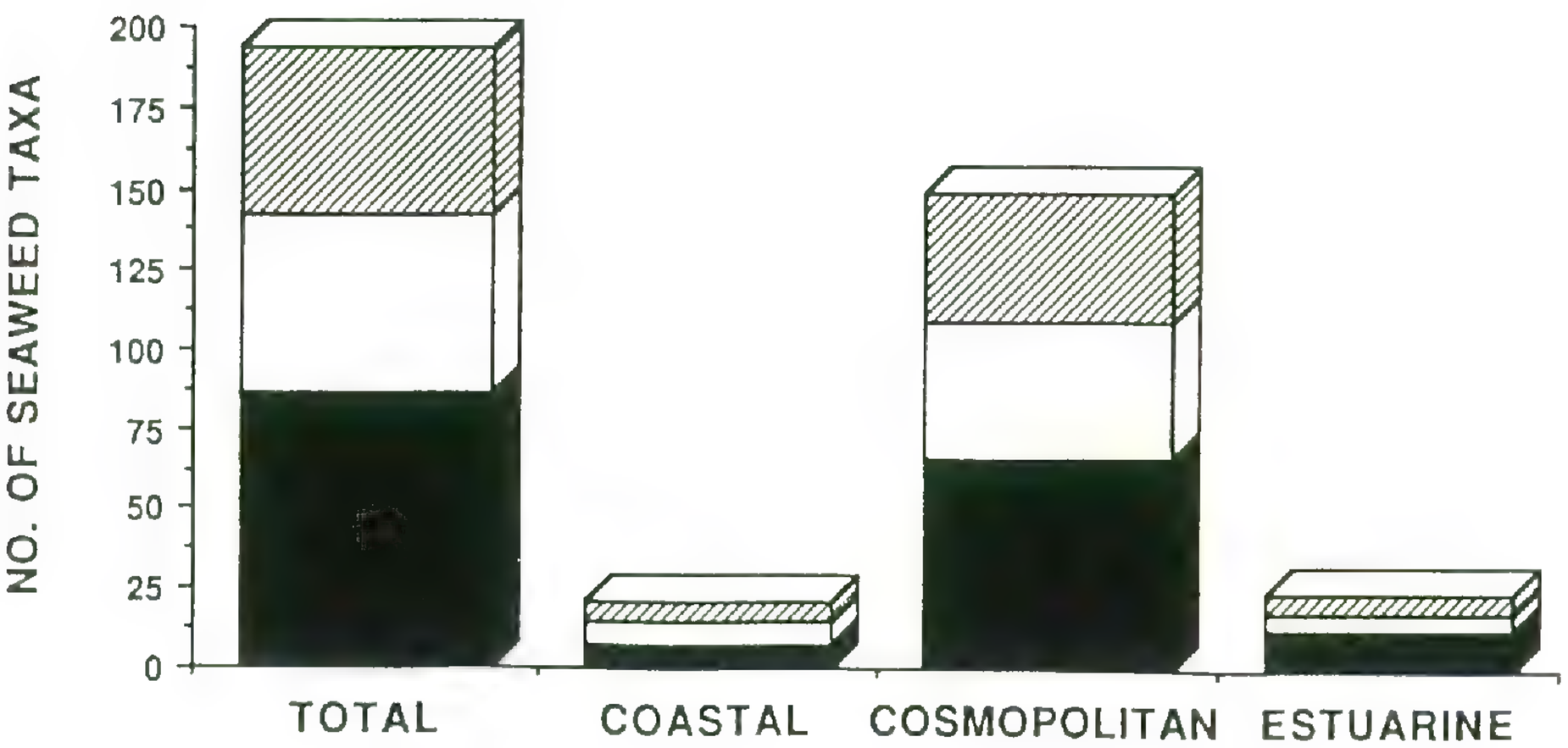
GOLETA SLOUGH AREA (CALIFORNIA)



YORK RIVER ESTUARINE AREA (MAINE)



GREAT BAY ESTUARINE AREA (NH/MAINE)



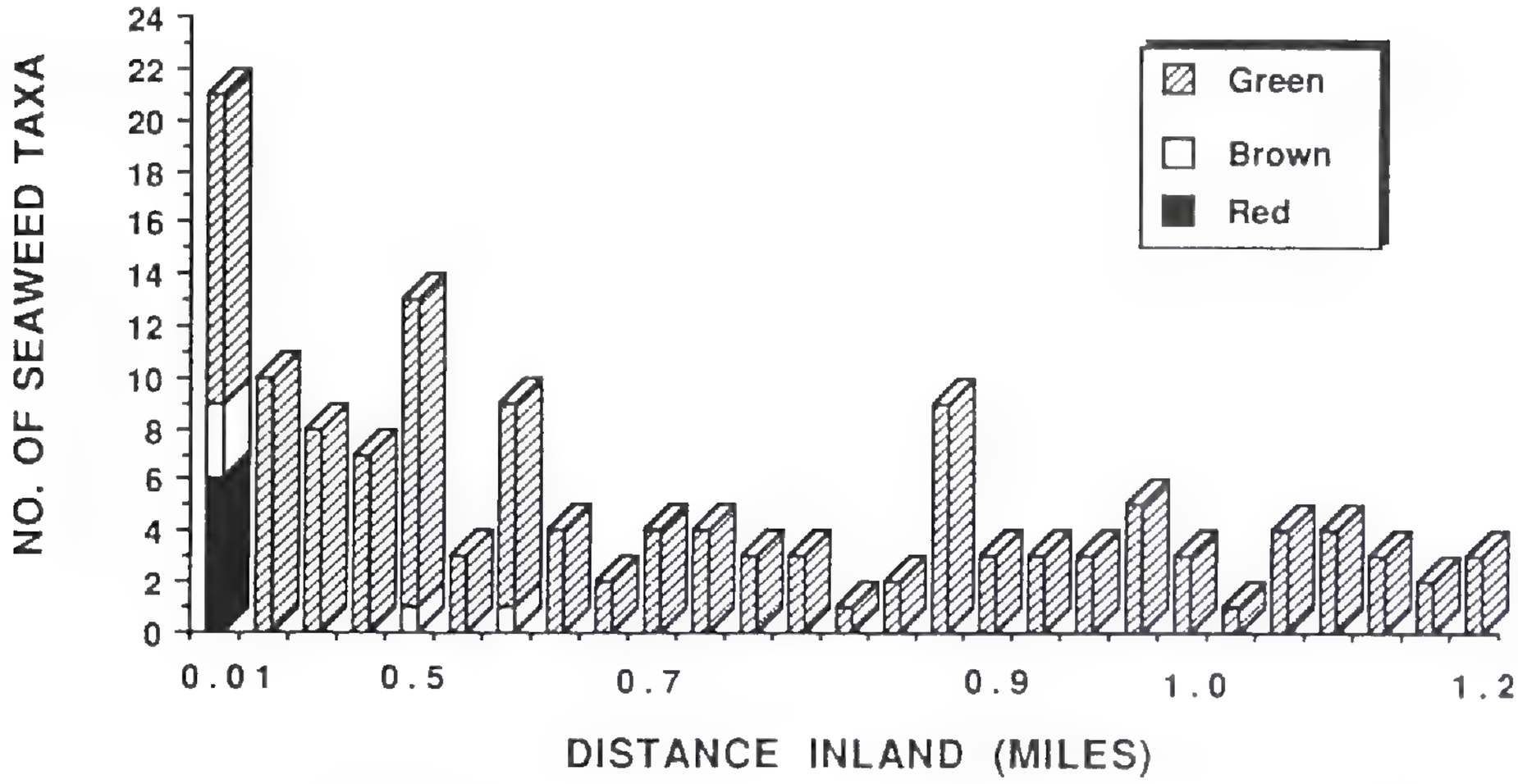


Figure 6. Number of seaweed taxa/site (green, brown and red) at twenty-seven Goleta Slough stations.

yond site 1, occurring also at sites 5 and 6 (i.e., 11.1% occurrence). See Table 2 for further details.

The paucity of seaweed taxa within Goleta Slough is further documented by comparing its species composition and mean number of taxa/site (Figure 7 and Table 2) with thirteen New England estuaries. Only 26 seaweeds were recorded from the Slough, with a mean of just 5.1 ± 4.3 taxa/site. Inner riverine habitats like the Winnicut River (4 taxa and 1.3 ± 1.6) have less diverse floras, while outer and mid-estuarine sites typically have greater number of species: e.g., Oyster (49 taxa and 12.6 ± 7.9), York (72 taxa and 21.4 ± 3.2) and Piscataqua Rivers (143 and 25.3 ± 24.9). Figure 8 compares the green algal taxa within the Slough (16 taxa) and thirteen New England estuaries. The number of taxa ranged from 24–37 within outer and mid-estuarine New England sites versus 12–20 for inner locations. The % of Slough greens within the same New England sites varied from 25–81%, with most habitats, other than the Winnicut and Merrimack Rivers, having floristic affinities of 50% or more. None of the browns

←

Figure 5. A comparison of species richness and local distribution of seaweed taxa from the Goleta Slough and adjacent open coast (California) with the York River (Maine) and the Great Bay Estuarine areas (Maine-New Hampshire).

Table 2. Summary of seaweed taxa at twenty-seven sites within the Goleta Slough.

	1	2	3	4	5	6	7	8	9	10	11
Chlorophyta											
Blidingia minima	x	x	x	x	x	x		x			
Capsosiphon fulvescens		x	x		x						
Chaetomorpha aerea	x										
Cladophora microcladioides	x										
Cladophora sericea	x	x	x		x	x					
Enteromorpha clathrata	x	x	x	x	x	x	x		x		x
Enteromorpha compressa	x			x	x			x			
Enteromorpha flexuosa ssp. *flexuosa*	x	x		x	x	x					
Enteromorpha intestinalis	x				x	x					
Enteromorpha linza		x									
Enteromorpha prolifera			x	x	x	x					x
Microspora pachyderma		x	x		x			x	x	x	
Rhizoclonium riparium	x	x	x	x	x	x	x		x		x
Ulva lactuca	x	x			x						
Ulva taeniata	x										
Ulvaria oxysperma	x	x	x	x	x	x					
# Green algal taxa/site	12	10	8	7	12	8	2	3	3	1	3
Mean # (± SD) green algal taxa/site (4.7 ± 3.1)											
Mean % occurrence (± SD) green algal taxa (28.9% + 24.6%)											
Total # green algal taxa (16)											
Phaeophyta											
Ectocarpus parvus	x				x	x					

Table 2. Extended.

12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	%*
x	x							x							x	40.7
										x					x	18.5
																3.7
																3.7
			x					x							x	29.6
x	x		x	x	x	x	x	x	x	x	x	x		x	x	85.2
															x	18.5
		x		x		x				x		x	x			40.7
					x											14.8
						x	x			x		x		x	x	40.7
		x	x												x	33.3
x	x	x	x	x	x	x	x	x		x	x		x	x	x	81.5
																11.1
																3.7
	x						x								x	33.3
3	4	3	4	3	3	4	4	4	1	5	2	3	2	3	9	
																11.1

Table 2. Continued

	1	2	3	4	5	6	7	8	9	10	11
Endarachne binghamiae	x										
Taonia lennebackerae	x										
# Brown algal taxa/site	3	0	0	0	1	1	0	0	0	0	0
Mean # (± SD) brown algal taxa/site (0.19 ± 0.61)											
Mean % occurrence (± SD) brown algal taxa (6.2% ± 3.5%)											
Total # brown algal taxa (3)											
Rhodophyta											
Chondria nidifica	x										
Gelidium coulteri	x										
Gigartina canaliculata	x										
Gigartina leptorhynchos	x										
Polysiphonia hendryi	x										
Pterosiphonia dendroidea	x										
Stylonema alsidii	x										
# Red algal taxa/site	7	0	0	0	0	0	0	0	0	0	0
Mean # (± SD) red algal taxa/site (0.26 ± 1.32)											
Mean % occurrence (± SD) red algal taxa (3.7% ± 0%)											
Total # red algal taxa (7)											
Total seaweed taxa/site	22	10	8	7	13	9	2	3	3	1	3
Mean # (± SD) total seaweed taxa/site (5.1 ± 4.4)											
Total seaweed taxa (26)											

* The % values represent calculations based upon 27 Goleta Slough stations.

Table 2. Extended. Continued.

12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	%*
																3.7
																3.7
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
																3.7
																3.7
																3.7
																3.7
																3.7
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
3	4	3	4	3	3	4	4	4	1	5	2	3	2	3	9	

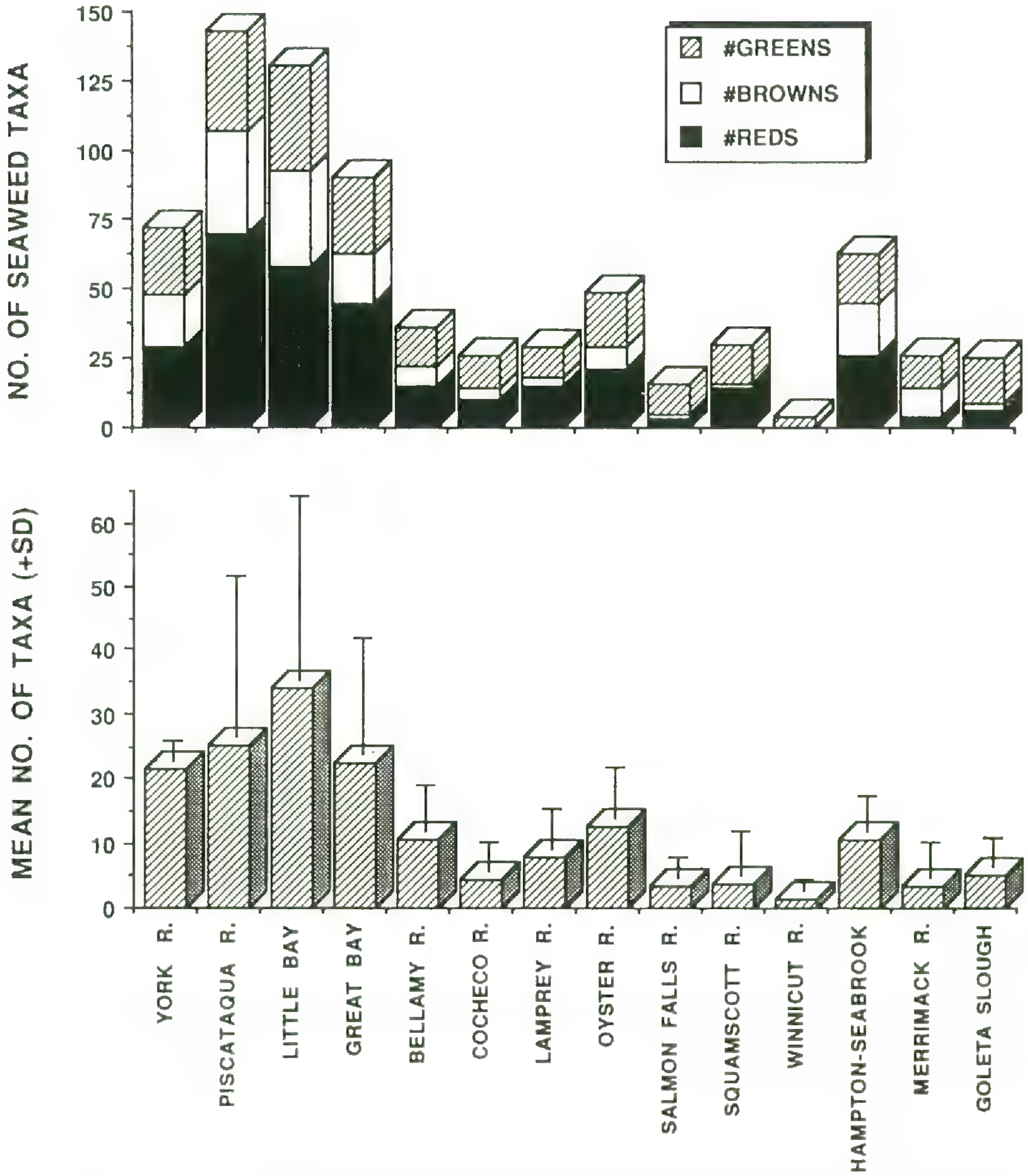


Figure 7. A comparison of the Goleta Slough flora and thirteen other New England estuarine habitats, expressed as the total number of green, brown and red algae/site as well as the mean (± SD) number of total taxa/site.

and only one red alga (*Stylonema alsidii*) occurred in both the Slough and New England estuaries.

PHENOLOGICAL PATTERNS AT GOLETA POINT

Table 3 summarizes monthly occurrences of seaweed taxa on the Goleta Point transect. No conspicuous pattern was evident, except that the minimum number of taxa occurred in April (27) and the highest in February and November (45). Green algae

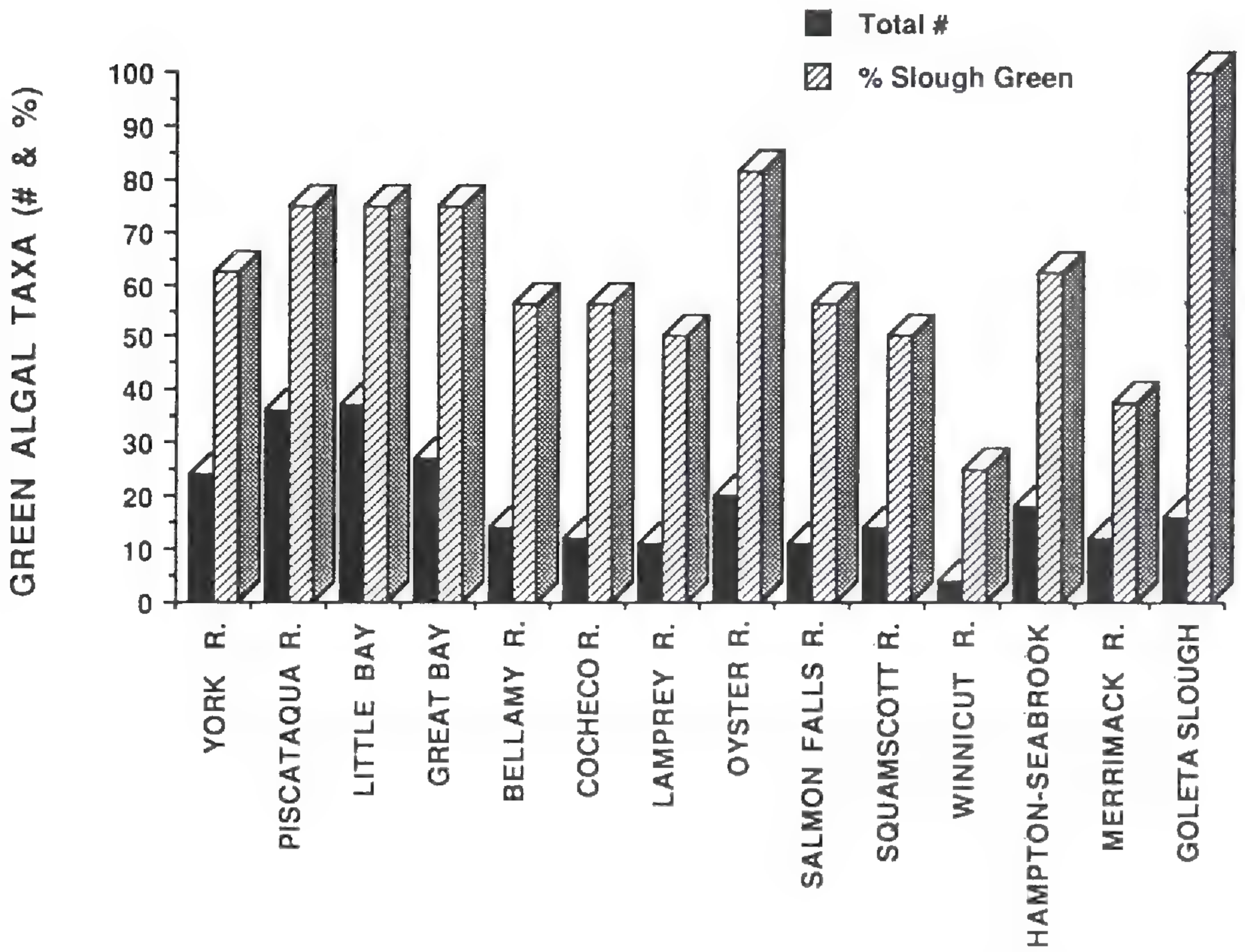


Figure 8. A comparison of the green algal floras of the Goleta Slough and thirteen other New England estuarine habitats, expressed as the total number of green algae as well as the % of Goleta Slough taxa.

varied from 5–12 taxa/month versus 3–9 for the browns and 23–29 for the reds. The mean number of taxa/month was 39.2 ± 6.0, with reds contributing 24.7 (± 2.8), greens 8.4 (± 2.1) and browns 6.1 (± 2.4). Four species were collected each month (i.e., *Gelidium coulteri, Gigartina canaliculata, G. leptorhynchos, Pterosiphonia dendroidea*). Thirteen others occurred during eight of nine months (90% occurrence), including *Chaetomorpha aerea, Cladophora columbiana, Ulva taeniata, Egregia menziesii, Endarachne binghamiae, Scytosiphon dotyi, Centroceras clavulatum, Ceramium eatonianum, Corallina vancouveriensis, Cryptopleura violacea, Gastroclonium subarcticulatum, Gigartina volans* and *Polysiphonia hendryi*. By contrast, 30 of the 94 taxa were only found once (~32% of total flora).

ABUNDANCE PATTERNS WITHIN GOLETA SLOUGH

Figure 9 illustrates the abundance of green algae and the California horn snail (*Cerithidea californica*) within three shallow

Table 3. Monthly records of seaweed taxa on Goleta Point transect.

	J	F	M	A	M	J	J	A	S	O	N	D	%*
Chlorophyta													
Acrochaete viridis							x						11.1
Blidingia minima			x	x			x	x					44.4
Bryopsis corticulans		x											11.1
Bryopsis hypnoides								x			x		22.2
Chaetomorpha aerea	x	x	x		x	x	x	x			x		88.9
Cladophora columbiana	x	x	x		x	x	x	x			x		88.9
Cladophora graminea								x					11.1
Cladophora sericea	x	x	x		x						x		55.6
Codium sp. (basal filaments)	x												11.1
Enteromorpha clathrata		x			x	x	x	x			x		66.7
Enteromorpha compressa	x			x	x	x	x	x			x		77.8
Enteromorpha flexuosa ssp. *flexuosa*		x			x			x					33.3
Enteromorpha linza	x	x		x			x	x			x		66.7
Enteromorpha prolifera		x	x	x		x	x	x					66.7
Rhizoclonium implexum		x											11.1
Ulva californica		x		x	x								33.3
Ulva lactuca			x			x	x	x			x		55.6
Ulva taeniata	x	x	x		x	x	x	x			x		88.9
# Green algal taxa/month	7	11	7	5	8	7	10	12			9		
Mean # (± SD) green algal taxa/month (8.4 ± 2.1)													
Total green algal taxa (18)													
Phaeophyta													
Colpomenia sinuosa	x		x										22.2

Table 3. Continued.

	J	F	M	A	M	J	J	A	S	O	N	D	%*
Cylindrocarpus rugosus	x	x			x			x					44.4
Ectocarpus parvus	x	x					x	x			x		55.6
Egregia menziesii	x		x	x	x	x	x	x			x		88.9
Endarachne binghamiae	x	x	x	x		x	x	x			x		88.9
Giffordia sandriana			x				x	x			x		44.4
Hincksia granulosa	x	x											22.2
Scytosiphon dotyi	x	x	x	x	x		x	x			x		88.9
Scytosiphon lomentaria			x		x								22.2
Sphacelaria didichotoma		x	x								x		33.3
Taonia lennebackerae	x	x	x								x		44.4
Zonaria farlowii	x	x	x		x						x		55.6
# Brown algal taxa/month	9	8	9	3	5	2	5	6			8		
Mean (# (± SD) brown algal taxa/month (6.1 ± 2.4)													
Total brown algal taxa (12)													
Rhodophyta													
Ahnfeltia fastigiata		x	x	x	x		x	x			x		77.8
Antithamnion defectum								x					11.1
Asterocolax gardneri		x											11.1
Audouinella daviesii		x											11.1
Bangia vermicularis			x										11.1
Bossiella orbigniana ssp. *dichotoma*		x				x	x						33.3
Bossiella orbigniana ssp. *orbigniana*				x									11.1
Centroceras clavulatum	x	x	x		x	x	x	x			x		88.9
Ceramium californicum											x		11.1

Table 3. Continued.

	J	F	M	A	M	J	J	A	S	O	N	D	%*
Ceramium eatonianum	x		x	x	x	x	x	x			x		88.9
Ceramium sinicola		x											11.1
Chondria nidifica	x	x					x	x			x		55.6
Corallina officinalis var. *chilensis*		x											11.1
Corallina vancouveriensis	x	x	x	x	x	x	x	x			x		88.9
Cryptopleura corallinara											x		11.1
Cryptopleura crispa				x									11.1
Cryptopleura violacea	x		x	x	x	x	x	x			x		88.9
Cumagloia andersonii					x	x	x	x					44.4
Erythrotrichia carnea	x		x								x		33.3
Gastroclonium subarticulatum	x	x	x	x	x	x	x				x		88.9
Gelidiocolax microsphaerica	x												11.1
Gelidium coulteri	x	x	x	x	x	x	x	x			x		100
Gelidium pusillum	x	x					x						33.3
Gigartina canaliculata	x	x	x	x	x	x	x	x			x		100
Gigartina leptorhynchos	x	x	x	x	x	x	x	x			x		100
Gigartina ornithorhynchos					x		x	x					33.3
Gigartina volans		x	x	x	x	x	x	x			x		88.9
Gracilaria papenfussii	x		x	x	x		x				x		66.7
Gracilaria textorii var. *cunninghamii*	x		x		x			x			x		55.6
Gracilariophila oryzoides	x												11.1
Grateloupia doryphora				x	x	x	x	x					55.6
Gymnogongrus chiton											x		11.1
Gymnogongrus leptophyllus	x	x											22.2
Herposiphonia secunda forma *tenella*		x											11.1

Table 3. Continued.

	J	F	M	A	M	J	J	A	S	O	N	D	%*
Herposiphonia verticillata		x											11.1
Holmesia californica						x							11.1
Janczewskia lappacea	x						x	x					33.3
Laurencia pacifica						x		x					22.2
Laurencia spectabilis	x	x	x	x	x						x		66.7
Mastocarpus papillatus					x		x						22.2
Melobesia marginata											x		11.1
Melobesia mediocris						x							11.1
Microcladia coulteri				x			x						22.2
Nemalion helminthoides					x	x	x	x			x		55.6
Nienbergia andersoniana		x									x		22.2
Pogonophorella californica			x										11.1
Polysiphonia hendryi	x	x	x	x		x	x	x			x		88.9
Polysiphonia pacifica								x			x		22.2
Polysiphonia scopulorum var. *villum*	x												11.1
Porphyra perforata			x	x	x	x	x	x					66.7
Prionitis lanceolata				x									11.1
Pterochondria woodii	x					x							22.2
Pterosiphonia baileyi	x		x				x				x		44.4
Pterosiphonia dendroidea	x	x	x	x	x	x	x	x			x		100
Rhodoglossum affine					x	x	x	x			x		55.6
Rhodoglossum californicum							x						11.1
Rhodymenia pacifica		x	x										22.2
Sarcodiotheca gaudichaudii		x	x		x		x	x					55.6
Scinaia articulata						x							11.1

Table 3. Continued.

	J	F	M	A	M	J	J	A	S	O	N	D	%*
Scinaia confusa								x					11.1
Schizymenia pacifica			x		x								22.2
Smithora naiadum		x	x		x	x	x				x		66.7
Stenogramme interrupta													11.1
Stylonema alsidii		x						x			x		22.2
# Red algal taxa/month	23	26	24	19	24	23	29	26			28		
Mean # (± SD) red algal taxa/month (24.7 ± 2.8)													
Total red algal taxa (64)													
Total # taxa/month	39	45	40	27	37	32	44	44			45		
Mean # (± SD) total taxa/month (39.2 ± 6.0)													
Total seaweed taxa (94)													

* The % values represent calculations based upon a total of nine monthly samples.

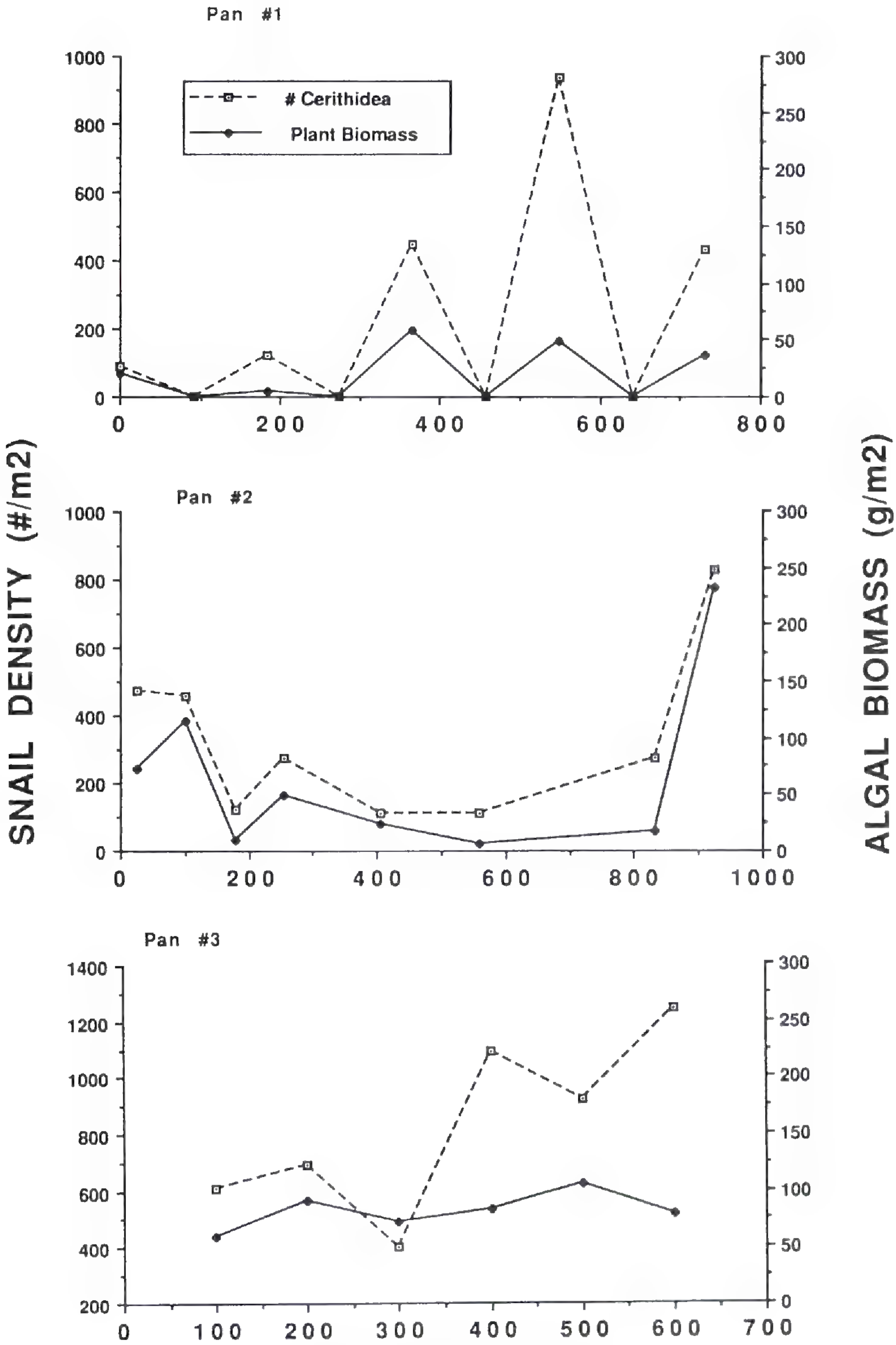


Figure 9. Spatial patterns of green algal biomass (g dry weigh/m^2) and horn snail densities (#/m^2) within three shallow Goleta Slough pans.

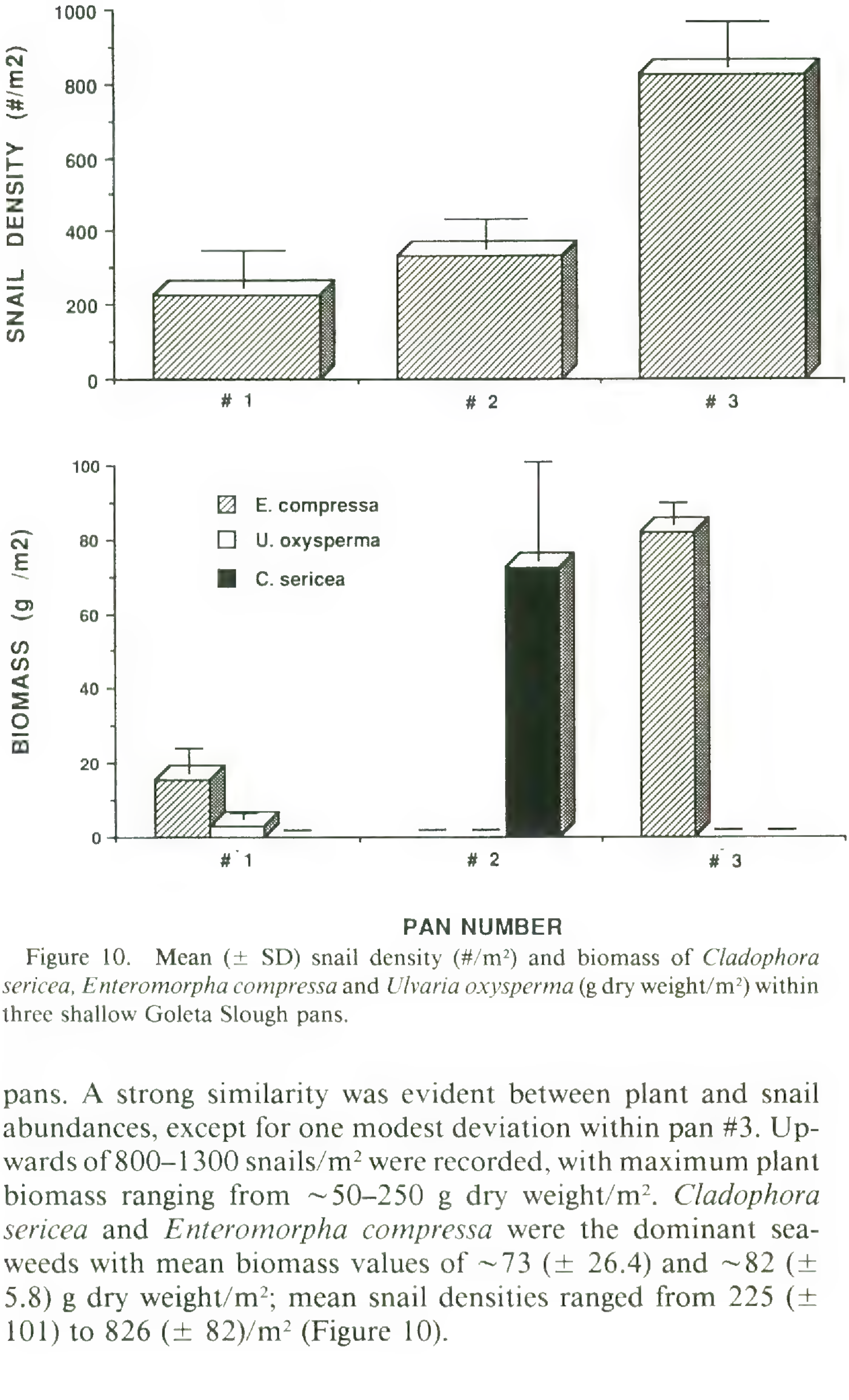


Figure 10. Mean (± SD) snail density (#/m²) and biomass of *Cladophora sericea*, *Enteromorpha compressa* and *Ulvaria oxysperma* (g dry weight/m²) within three shallow Goleta Slough pans.

pans. A strong similarity was evident between plant and snail abundances, except for one modest deviation within pan #3. Upwards of 800–1300 snails/m² were recorded, with maximum plant biomass ranging from ~50–250 g dry weight/m². *Cladophora sericea* and *Enteromorpha compressa* were the dominant seaweeds with mean biomass values of ~73 (± 26.4) and ~82 (± 5.8) g dry weight/m²; mean snail densities ranged from 225 (± 101) to 826 (± 82)/m² (Figure 10).

DISCUSSION

Patterns of species composition and richness of seaweeds at our study sites show strong contrasts (Figure 5), which may be associated with pronounced habitat and local environmental variability (Littler et al., 1991; Murray and Littler, 1989; Thom, 1976, 1980; Thom and Widdowson, 1978). Strong gradients of water motion, substratum availability and depth are evident from the offshore Naples reef site into the Goleta Slough, with deep water and abundant rocky substrata (former) versus muddy, shallow sedimented habitats (latter). The Goleta Point and Bay sites are exposed to contrasting (i.e., diminishing) patterns of water motion and sand fluctuation (Wheeler et al., 1981), with the latter often causing extensive erosion and burial at Goleta Point (Figure 3) and periodically blocking off the Slough (Macdonald, 1977; Onuf and Zedler, 1988). Contrasting patterns of light penetration are evident between Goleta Point and the Slough due to enhanced sedimentation (Wheeler et al., loc. cit.), while hydrographic differences between coastal and Slough habitats are most pronounced during summer (Figure 4). As would be expected, the most depauperate flora occurs within the Slough, a shallow, turbid and hydrographically variable environment (Zedler, 1982b). The most diverse flora was found at Goleta Point, which had a variety of intertidal and subtidal habitats, as well as intermediate conditions of light penetration, sediments and hydrographic variability. The Goleta Point transect was also the most extensively studied habitat (Table 3). The subtidal zone within the Slough is limited and shallow, while it is more expansive on the adjacent open coast. Typically, temperate subtidal habitats are dominated by a variety of red and brown algae, with ratios of greens to reds decreasing with depth (Dawson et al., 1960; Edelstein et al., 1969; Kain, 1960; Lamb and Zimmerman, 1964; Mathieson, 1979; Neushul, 1965; Sears and Wilce, 1974). By contrast, the Slough's flora is dominated by a few ephemeral green algae (Figure 6).

As noted previously, diversity of seaweeds near Goleta can be further documented using Cheney's (R + C)/P ratio. Three of the four study sites are interpreted as having "warm water" floras (~5.9–7.7), except for the offshore Goleta Bay site (2.0). Obviously, these floristic ratios are influenced by variability of habitat (see above) and species composition, with the highest value occurring within Goleta Slough (~7.7) where only three brown algae

were recorded. In comparing these ratios for New England sites, eleven outer and mid-estuarine locations had values of < 6.0, indicating "mixed" or "cold-water" floras, while three inner riverine habitats (i.e., Lamprey, Salmon Falls and Squamscott Rivers), with reduced numbers of brown algal taxa, had ratios of 7–14 (cf. Mathieson and Penniman, 1986a, 1991). Adjacent open coastal sites in New England have much lower ratios (~1.72–3.0) and an overall mean value of ~2.5 (Mathieson and Penniman, 1986b). Such patterns confirm the usefulness of Cheney's ratio primarily for open coastal populations.

Based on a variety of detailed studies at 22 open coastal intertidal sites in southern California, Littler et al. (1991) recorded 224 taxa (i.e., 149 red, 47 brown and 23 green algae), while we recorded 152 at four primary sites (i.e., 104 red, 22 brown and 26 green algae). Our documentation of higher numbers of green algae and six new geographical records (see above) probably resulted from more extensive seasonal sampling of estuarine and subtidal habitats. In discussing distributional patterns of individual taxa, Littler et al. (loc. cit.) state that only 12 of the 224 seaweeds (i.e., exclusive of Cyanophyceae) occurred at all 22 sites, with these consisting of corallines, sheet-like species and small filamentous algae (Stewart, 1982, 1983). Most other taxa had restricted distributions, reflecting the high degree of local environmental variability between habitats (Murray and Littler, 1989). Both studies document a diverse warm-temperature flora dominated by red algae (Lüning, 1990; Thom, 1976, 1980) with restricted occurrences of several taxa. Littler and colleagues (loc. cit.) note that subclimax assemblages occur where there is a lack of environmental constancy (e.g., fluctuating sand) or some form of physiological stress (e.g., domestic pollution). In such habitats, opportunistic species readily occupy newly opened space (Emerson and Zedler, 1978; Murray and Littler, 1978; Wilson, 1925). If disturbance is periodic and not too severe, intertidal populations exhibit increased densities due to coexistence of both early and late successional species (Sousa, 1979). Such patterns probably occur at Goleta Point, where a large number of epiphytic and "turf" forms (Stewart, 1982, 1983), as well as the highest number of taxa/site, are found.

Our floristic records for open coastal taxa can be compared with several previous studies near Goleta and throughout southern California (e.g., Dawson, 1959a, 1959b, 1965; Murray and

Littler, 1989; Nicholson and Cimberg, 1971). For example, Dawson and Nicholson and Cimberg (loc. cit.) recorded intertidal species composition at three contiguous points near Goleta (Figure 1), with the former recording 38 and 47 seaweed taxa/site at Goleta and Santa Barbara Points, respectively and the latter, 49 taxa at Devereaux Point. Murray and Littler (loc. cit.) documented seasonal collections at 21 rocky intertidal sites between Government Point (Santa Barbara County) and Ocean Beach (San Diego County), finding a range of 51–107 taxa/site and a mean of 76.3 ± 15.5. In addition, they recorded 93 taxa at Devereaux Point, consisting of 69 red, 15 brown and 9 green algae. Dawson's collections of "dominant intertidal seaweeds" at Goleta Point (38 taxa) were based upon three seasonal collections (winter, spring and fall), while ours (i.e., 94 taxa) were made during nine monthly collections, which included all conspicuous taxa from an intertidal and shallow subtidal transect. Thirty of these 94 taxa (i.e., ~32%) were only collected once (Table 3), giving a mean value of 39.2 ± 6.0 taxa/month. The latter value is almost identical to Dawson's report. Overall, our records from Goleta Point are very similar to those of Murray and Littler (loc. cit.) from Devereaux Point (~93 taxa), while they are much higher than Dawson's from Goleta Point. Unfortunately, further comparisons are difficult because of varying collecting methods and sampling frequencies. Even so, eight of Dawson's "common intertidal" taxa from Goleta Point were never found by us at any of our four sites (i.e., *Anisocladella pacifica, Callophyllis obtusifolia, Chondria decipiens, Corallina pinnatifolia, Cryptopleura lobulifera, Gracilaria lemaneiformis, Laurencia splendens* and *Pleonosporium squarrulosum*), while Murray and Littler (loc. cit.) found half of these taxa at Devereaux Point. Thus, four of Dawson's common taxa may have become less so, while other specific changes may have occurred (Widdowson, 1971).

Estuarine reductional and compositional patterns observed within the Goleta Slough (Figure 6) are fairly typical (Coutinho and Seeliger, 1984; Josselyn and West, 1985; Ketchum, 1983; Mathieson and Penniman, 1986a; Wilkinson, 1980); even so, the rate of species loss upstream and dominance by ephemeral green algae are more pronounced within the Slough than in San Francisco Bay (Josselyn and West, loc. cit.; Silva, 1979) and most New England estuaries (Figure 7). For example, most open coastal red and brown algae within the Slough dropped out after ~0.09 miles.

By contrast, Silva (loc. cit.) found that 125 of the 156 total taxa recorded from San Francisco Bay penetrated the central Bay, while the remainder were protected water species (estuarine) that were more prevalent in the Bay than on the open coast. In New England open coastal taxa extend inland about one mile on the tidal portions of the Merrimack River in Massachusetts (Mathieson and Fralick, 1973), ~2–3 miles on the York River in Maine (Mathieson et al., 1993) and ~8.5 miles on the Piscataqua River in New Hampshire (Mathieson et al., 1983; Reynolds and Mathieson, 1975). Of the three New England sites, the Piscataqua River has the strongest currents (~5.0 knots) and most abundant rocky substrata, while industrial development and eutrophication are limited on the York, moderate on the Piscataqua, and maximal on the Merrimack (Mathieson et al., 1993). Several physical factors are probably responsible for the pronounced truncation of species within Goleta Slough. Both the range of salt content and maximum salinities are greater (i.e., ~0–68‰, Figure 4) than those found within the entire Great Bay Estuary (i.e., all ten subareas), which vary from ~0–34‰ (Mathieson and Hehre, 1986; Norall et al., 1982). Goleta's arid climate and the Slough's restricted tidal exchange (i.e., via sand deposition) no doubt contribute to these high salinities (Macdonald, 1977; Onuf, 1987; Onuf and Zedler, 1988; Zedler, 1982b). Maximum surface water temperatures within the Great Bay system are less than those in the Slough, but they exhibit a greater seasonal amplitude, varying from ~−2.0°–27.0°C in the former (Mathieson and Hehre, loc. cit.) to ~14°–35°C in the latter (Figure 4). The Slough's shallow topography and limited solid substrata also contribute to its reduced and patchy flora, as well as its dominance by loose-lying and epiphytic seaweeds (Josselyn and West, 1985; Norton and Mathieson, 1983).

In contrast to the depauperate flora of the Goleta Slough (i.e., 26 taxa and 5.1 ± 4.3 taxa/site), most New England habitats are more diverse, particularly outer- and mid-estuarine sites like the York (72 taxa and 21.4 ± 3.2) and Piscataqua Rivers (143 and 25.3 ± 24.9) and Little (130 and 34.1 ± 29) and Great Bays (90 and 22.5 ± 18.0). Depauperate floras dominated by green algae may also occur within inner riverine sites like the Cocheco, Salmon Falls and Winnicut Rivers (i.e., 1.3 ± 1.6 to 4.5 ± 4.3 taxa), as well as within the outer tidal portions of the Merrimack River (3.5 ± 5.2). The latter is badly polluted and one of the largest

sources of freshwater discharge into the Gulf of Maine (Anon., 1984, 1987; Appolonio, 1979; Jerome et al., 1965; Lyons et al., 1982; Mathieson and Fralick, 1973; Miller et al., 1971). Comparing estuarine macroalgal communities within San Francisco Bay, Josselyn and West (1985) found a range of 28–61 taxa/site beyond its central portion, with lowest numbers occurring in South Bay. They noted that six of the eight most widely distributed species were green algae (*Enteromorpha clathrata, E. intestinalis, E. linza, Ulva angusta, U. lactuca* and *Cladophora sericea*) and two reds (*Antithamnion kylinii* and *Polysiphonia denudata*). Our studies of the Goleta Slough (Figure 8 and Table 2), plus those of Zedler (1982a, 1982b) from the Tijuana Estuary near San Diego and Norris (1970) from Elkhorn Slough near Carmel Bay, confirm a similar dominance of many of these same ephemeral green algae. Dawson (1962) found many of the same taxa (i.e., 9 green, 4 brown and 29 red algae) within the more saline Bahia de San Quintin. In summary, the Goleta Slough's flora is primarily dominated by ephemeral green algae and contains no perennial reds or browns; thus, it is analogous to several shallow embayments (estuaries) along the Pacific Coast of the U.S.A. and in New England (Figure 8).

As noted by several investigators (Anon., 1964; Clokie and Boney, 1980; Daly and Mathieson, 1977; Edwards, 1972; Littler, 1980; Littler et al., 1991; Patrick, 1963, 1964; Round, 1981; Wilkinson, 1980; Zedler, 1982b), patterns of low species richness are typical responses to stress, often allowing only a few tolerant species to dominate in both numbers and biomass. For example, the abundance of such ulotrichalean green algae as *Ulva lactuca, Enteromorpha* and *Ulvaria* (*Monostroma*) spp., typifies many eutrophied estuarine habitats, including the Goleta Slough (Cotton, 1910; Fritsch, 1956; Sawyer, 1965). The latter are tolerant of extremes of pollution and gross fluctuations in hydrographic conditions. Similar patterns are found in several estuaries having pronounced hydrographic variability and high sedimentation, including the Chesapeake Bay (Orris, 1980), the Merrimack River (Mathieson and Fralick, 1973) and many British and Dutch estuaries (Hartog, 1967; Nienhuis, 1975; Wilkinson, 1980). Within such turbid habitats, there is a relatively small pool of common (cosmopolitan) estuarine species, including *Cladophora, Enteromorpha,* and *Ulva* spp., together with several ceramialean red algae (Munda 1969, 1972; Orris, 1980; Wilkinson, 1980). The

similarity of the Slough's green algal flora to New England estuarine vegetation is striking, with most sites exhibiting floristic affinities of 50% or more (Figure 8). In discussing salt marsh vegetation (i.e., angiosperms) within southern California, Zedler (1982b) describes a rather limited and highly stressed community from several hypersaline marshes, while Onuf and Zedler (1988) state that six of the seven species and all of the genera listed by Reimold (1977) from the eastern United States are in common. Thus, the estuarine chlorophycean and angiosperm floras of the two regions exhibit reduced numbers of taxa but strong floristic similarities. Only one other seaweed, the red alga *Stylonema alsidii,* occurred both within the Slough and in New England estuarine habitats, while 18 other cosmopolitan and coastal taxa from the Goleta and Santa Barbara area were in common to New England (~13.0% of 146 taxa). These include 13 green (*Acrochaete viridis, Blidingia minima, Chaetomorpha aerea, Cladophora sericea, Codium fragile, Enteromorpha clathrata, E. compressa, E. intestinalis, E. linza, E. prolifera, Rhizoclonium riparium, Ulva lactuca* and *Ulvaria oxysperma*), 2 brown (*Desmarestia viridis* and *Scytosiphon lomentaria*) and 3 red algae (*Audouinella daviesii, Erythrotrichia carnea* and *Nemalion helminthoides*).

Describing seasonal variability of southern California seaweeds, Widdowson (1971) notes a conspicuous maximum in March–June and a minimum during August–September, due to changes of individual species that are present year-round. We found a rather irregular pattern on the Goleta Point transect (Table 3), which may have resulted from pronounced sand fluctuations (Figure 3). Dawson (1965) states that no conspicuous seasonal differences in quantity and quality of southern California seaweeds occur. Littler et al. (1991) emphasize that local-scale or even site-specific conditions predominate and they often obscure broad climatic effects. Thus, major stochastic abiotic disturbances may be more important than subtle seasonal patterns, including heavy precipitation and flooding, extreme atmospheric conditions during daylight tidal emersions, storm generated waves and sand burial/scouring (see above). More pronounced seasonal patterns are often evident within cold-temperate areas like New England (Mathieson, 1989; Mathieson and Penniman, 1986a).

As noted by Zedler (1980, 1982a, 1982b), algal mats are often conspicuous and productive components of southern California

tidal marshes, owing to the open canopies and short stature of their vascular plants. Two green algae (i.e., *Enteromorpha clathrata* and *Rhizoclonium riparium*), plus a variety of microscopic diatoms and blue greens, dominate the Tijuana Estuary near San Diego (Zedler, loc. cit.), while an analogous benthic microflora plus *Enteromorpha* and *Ulva* are abundant within the Mugu Lagoon near Port Hueneme (Onuf, 1987). According to Rudnicki (1986), maximum standing crops of dominant green algae within the Tijuana Estuary average 15 g dry wt./m^2, which is much less than the above ground biomass (~100–1100 g) of associated vascular plants (Zedler, 1982b). Green algal mats within the Goleta Slough were primarily composed of *Cladophora sericea* and *E. clathrata,* with mean biomass values of ~73 and 82 g dry wt./m^2, respectively (Figure 10). Such values are ~5.0–5.5 times greater than equivalent green algal mats within the Tijuana Estuary (Rudnicki, loc. cit.), and those of *E. clathrata* from San Francisco Bay (Shellem and Josselyn, 1982); they are also ~20–60 times greater than mid-estuarine *Enteromorpha* spp. and *Ulva lactuca* populations from New England (Chock and Mathieseon, 1983). By contrast, standing crop values for Goleta Slough macroalgae are approximately the same as those found within New England inner riverine sites such as the Oyster River (Mathieson, unpubl. data). Fucoid algae typically dominate New England mid-estuarine habitats, with *Ascophyllum nodosum* ecad *scorpioides* and *A. nodosum* having mean biomass values of ~300 and 500 g dry wt./m^2, respectively (Chock and Mathieson, loc. cit.). Thus, green algal standing stocks within the Slough are substantial but less than those of southern California vascular plants and New England estuarine fucoid algae.

The high densities of the California horn snail *Cerithidea californica* within the Goleta Slough (~225–826 snails/m^2) should be emphasized as well as the similarity of distributional patterns to *Cladophora sericea* and *Enteromorpha clathrata* (Figure 9). Among others, McCloy (1979) and Macdonald (1969) record high densities of horn snails (250 to $>$ 1000/m^2) from southern California marshes, while Morris et al. (1980) state that it is probably the most common estuarine snail within this geography, often forming dense aggregations under debris and amongst plants on high lagoonal mudflats. Several investigators (e.g., Morris et al., loc. cit.; Onuf, 1987; Whitlatch and Obrebski, 1980) suggest that *C. californica* primarily feeds upon microorganisms and fine or-

ganic detritus. By contrast, Dawson (1962) states that *Enteromorpha* and other green algae serve in considerable part as food for this extremely abundant snail, while Zedler (1982b) describes an enhancement of macroalgal biomass within the Tijuana Estuary after the exclusion of horn snails (i.e., via cages). She further states that the removal of horn snails by shore birds results in increased algal mats, while *in situ* patchiness of snails and intertidal algal mats may be due to feeding by birds and other carnivores. The distributional patterns of *C. californica* are analogous to those of the common mud snail *Ilyanassa obsoleta,* which occurs in aggregated masses on mudflats and other estuarine habitats on the east coast of North America (Morris, 1947; Smith, 1964). Similarly, the removal of *I. obsoleta* from intertidal mudflats in Georgia resulted in enhanced algal and microbial biomass (Pace et al., 1979). Whether the abundance of *C. californica* within Baja and southern California marshes (Barnard, 1962; Dawson, 1962; Morris et al., 1980; Zedler and Nordby, 1986) indicates a consistent and similar interaction with seaweeds like that of *I. obsoleta* and *Littorina* spp. on the east coast (Mathieson et al., 1991; Pace et al., loc. cit.), should be better clarified by exclusion and manipulative experiments. In a discussion of the shore crab *Hemigrapsus oregonensis,* Onuf (1987) states that it is capable of shredding live macrophytes and will grow well in the laboratory provided solely with *Enteromorpha* (Kuris and Mager, 1975). However, in nature it feeds on diatoms (Morris et al., 1980) and is a scavenger and predator (Chapman et al., 1982). Lastly, the interrelationship between green algae and some surface-feeding shorebirds (e.g., coots) within Mugu Lagoon should be noted, as they primarily feed on thick mats of *Enteromorpha* (Onuf, 1987).

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DEPARTMENT OF PLANT BIOLOGY
JACKSON ESTUARINE LABORATORY
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NEW HAMPSHIRE, 03824

APPENDIX: STUDY SITES

Open Coast

GP: Goleta Point: A semi-exposed sandy habitat also called Campus Point located at the west end of Goleta Bay (Dawson, 1959a, 1959b). Scattered rock outcrops (Monterey shale/siltstone) and boulders occur on a broad sandy beach, many of which are extensively scoured. The point is exposed to greater longshore currents and wave action than within Goleta Bay (Wheeler et al., 1981). Subtidal collections (−10 to −30 feet) were made just offshore from the Point (= 0 miles inland; 30–32‰, 14.0°–18.0°C).

GB: Goleta Bay: A coastal site having limited wave action and currents (see above). Substratum primarily consists of sand with scattered boulders; sand often covers *in situ* benthic populations. Collections were made from −5 to −50 feet near two experimental farm sites (cf. Wheeler et al., 1981) (= just offshore from Goleta; 30–32‰, 14.0°–18.0°C).

NR: Naples Reef: An offshore reef site having abundant rocky substrata (Monterey shale/siltstone) and reduced levels of sediment and sand. Collections were made from −15 to −40 feet (= ~2.0 miles offshore from Santa Barbara Point).

Goleta Slough

1: Near the mouth of the Goleta Slough, just downstream from Goleta Beach State Pier; a sandy berm-like area on the northern bank of the channel. Collections were made from an old pier piling as well as on cliff facings with scattered mussel populations. The mouth of the slough is periodically blocked off by sand deposition during the summer, restricting tidal exchange (= 0.087 miles inland; 13–32‰, 15.0°–20.0°C).

2: A muddy area upstream from the mouth of the slough and near the entrance (i.e., bridge) to Goleta Beach State Park. Collections were made on the south bank of the channel, next to the park ranger's house. The substrata consists of muddy surfaces, as well as scattered and broken pieces of asphalt (= 0.311 miles inland, 27–30‰, 15.2°–21.5°C).

3: A muddy area on the south bank of the channel adjacent to the entrance to Goleta Beach State Park. Plants were collected from bridge pilings, scattered boulders, and as entangled masses on extensive muddy shorelines (= 0.392 miles inland; 2–25.5‰, 13.0°–15.3°C).

4: A muddy area near the Clarence Memorial Boulevard overpass (~0.125

miles) and upstream from the entrance to Goleta Beach State Park (~0.0623 miles). Collections were made on the south bank of the channel (= 0.448 miles inland; 1–33‰, 13.5°–20.5°C).

5: A muddy area on the south bank of a channel, ~0.075 miles from the Clarence Ward Memorial Boulevard overpass and near a bicycle overpass. A series of gas pipelines were also present. Collections were made of entangled masses of seaweeds on muddy surfaces, while epiphytic and entangled masses of algae also occurred within a small shallow pan (= 0.517 miles inland; 2–32‰, 15.2°–28.5°C).

6: Two shallow pans near station 7. Collections were made of free-floating and entangled masses of plants within the pans and on muddy surfaces around the periphery of the pan (= 0.622 miles inland; 11–42‰, 18.0°–32.0°C).

7: The south bank of a narrow muddy channel at the end of a large shallow pan, ~0.150 miles upstream from the Clarence Ward Memorial Boulevard overpass. Collections were made from entangled masses of seaweeds growing on muddy surfaces, epiphytic populations on *Salicornia virginica* and attached plants on drift wood (= 0.647 miles inland; 22‰, 15.4°–24.5°C).

8: A narrow tidal channel located approximately 0.3 miles upstream from the Clarence Ward Memorial Boulevard overpass on the south bank of the channel. The site is located at the end of an auxilliary road and just SW from the end of Santa Barbara's Municipal Airport runway 33L. Collections were made of epiphytic plants and entangled masses on muddy substrata (= 0.772 miles inland; 9–25‰, 17.0°–25.0°C).

9: A muddy channel approximately 0.375 miles upstream from the Clarence Ward Memorial Boulevard overpass on the south bank of the channel. The site is next to a pipe crossing. Collections were made on muddy vertical bankings (= 0.778 miles inland; 0–25‰, 15.5°–29.0°C).

10: One end of a large pan just downstream from the junction of two channels. Collections were made from emergent and tangled masses of seaweeds, which grew amongst vascular plants (= 0.996 miles inland; 0–12‰, 17.5°–26.0°C).

11: Junction of two tidal channels ~0.48 miles upstream from the Clarence Ward Memorial Boulevard overpass. Collections were made from entangled muddy plants (= 0.878 miles inland; 0–28‰, 17.8°–32.0°C).

12: A narrow muddy tidal channel, ~0.555 miles upstream from the Clarence Ward Memorial Boulevard overpass. Collections were made from entangled masses amongst *Salicornia virginica,* etc. (= 0.94 miles inland; 0–29‰, 23.0°–29.0°C).

13: A tidal channel ~0.2 miles downstream from a spill gate; considerable freshwater runoff was evident, particularly during spring. Collections were made along an embankment area lined with *Salicornia virginica* (= 1.058 miles inland; 0–29‰, 18.5°–30.5°C).

14: A large shallow pan next to the Goleta Water District facility. Stations 10 and 14 represent the extremities of the same pan. Collections were made from free-floating and entangled masses of seaweeds growing amongst vascular plants, as well as from entangled masses on muddy surfaces on the periphery of the pan (= 1.27 miles inland; 2–13‰, 19.5°–27.0°C).

15: A small pan area located just north of the spill gate adjacent to the Goleta Water District facility. Collections were made from free-floating and entangled masses of seaweeds, growing amongst vascular plants and on muddy marginal surfaces around the pans (= 1.114 miles inland; 6–>32‰, 21.0°–>30.0°C).

16: A shallow pan area, partially dried up during summer and forming cracked pavement-like masses of blue-green algae. Entangled masses of green algae were also present around the margin of the pan, growing amongst *Salicornia virginica*; many dead bivalve and periwinkle shells were found near these pans (= 0.977 miles inland; 13–68‰, 18.5°–32.0°C).

17: A shallow pan just upstream from station 5. Collections were made from entangled and free-floating masses of seaweeds growing in and around the pan (= 0.572 miles inland; 20–48‰).

18: A shallow pan area just upstream from station 17. Collections were similar to those at 17 (= 0.641 miles inland; 11–42‰, 18.0°–32.0°C).

19: A muddy channel bank next to station 18. Collections were made from entangled masses on muddy surfaces and around the bases of vascular plants (= 0.654 miles inland; 1–35‰, 14.5°–16.0°C).

20: A muddy channel bank that was artificially dredged and widened. Collections were made from entangled masses and carpets on the muddy channel surfaces and bankings (= 0.734 miles inland; 11–32‰, 14.5°–29.5°C).

21: A variety of shallow pans similar to station 16, although of a more extensive area (= 0.828 miles inland; 11–50‰, 24.0°–35.0°C).

22: A small channel downstream from station 23, approximately 15 feet wide with conspicuous freshwater drainage at low tide. Collections were made from small sticks and from entangled and tufted masses of seaweeds growing on muddy surfaces (= 0.942 miles inland; 12–25‰, 23.5°–32.0°C).

23: A muddy channel with abundant masses of green algae and vascular plants (= 0.840 miles inland; 35‰, 32.0°C).

24: The south bank of a wide, artificially dug channel near station 16, having limited seaweed populations (= 0.840 miles inland; 0–22‰, 22.5°–32.0°C).

25: A shallow pan area just north of and parallel to a bridge carrying pipes over a channel. Collections consisted mostly of entangled masses of seaweeds, growing on and amongst *Salicornia virginica* (= 0.940 miles; 0–>32‰, 23.8°–>30.0°C).

26: The northern bank of Glen Annie Creek, opposite station 24 and adjacent to a pipe crossing. A channel 25–30 feet wide with muddy surfaces covered with *Vaucheria* (= 1.145 miles inland; 24‰, 30.0°C).

27: Headwaters of the easternmost tidal channel in the Goleta Slough (Atascadero). It originates from San Pedro Creek and adjacent to the Clarence Ward Memorial Boulevard Highway. Collections were made near a concrete dam, and on adjacent scattered rocks and muddy bankings (= 0.846 miles inland; 0–10‰, 12.0°–28.5°C).

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ECOLOGY, REPRODUCTIVE BIOLOGY AND POPULATION GENETICS OF *OPHIOGLOSSUM VULGATUM* (OPHIOGLASSACEAE) IN MASSACHUSETTS

ROBERT T. MCMASTER

ABSTRACT

The northern adder's-tongue fern, *Ophioglossum vulgatum* var. *pseudopodum* (Blake) Farw. (Ophioglossaceae), occurs in five known populations in Massachusetts and has been designated as threatened by the Massachusetts Natural Heritage Program. The autecology, population biology and population genetics of *O. vulgatum* var. *pseudopodum* were analyzed during the summer of 1992. The distribution of each population was mapped, associated vegetation sampled, and permanent plots established for long-term study. Isozyme electrophoresis was employed to assess variability within and between populations. The historical distribution of the species in Massachusetts was examined based upon herbarium specimens. Each of the known Massachusetts populations is in an early successional site with a unique history of disturbance; sites include pasture, a power line right-of-way, and abandoned beaver meadows. Four of the five populations are small, ranging from 1 to 109 sporophytes. All specimens subjected to isozyme analysis were monomorphic for all loci examined. The implications of the spatial and temporal distribution, population size, and low genetic variability of *Ophioglossum vulgatum* var. *pseudopodum* are discussed. Management considerations for the preservation of this and other early successional species are suggested.

Key Words: *Ophioglossum vulgatum*, Ophioglossaceae, fern reproductive biology, population genetics, early successional species, rare plant species, self-fertilization, Massachusetts

INTRODUCTION

Ophioglossum vulgatum var. *pseudopodum* (Blake) Farw., the northern adder's-tongue fern (Ophioglossaceae), has a broad distribution, occurring throughout its range in a variety of wet and mesic habitats. In Massachusetts, *O. vulgatum* var. *pseudopodum* is known from over one hundred historical sites and as late as 1978 was thought to occur in all counties of the state (Coddington and Field, 1978). By 1985, however, with only four extant stations known, it was placed on the Massachusetts list of threatened species, a status which it holds at present (Massachusetts List of Endangered, Threatened and Special Concern Species, 1994). The species was listed as rare and endangered in Rhode Island in 1978 (Church and Champlin, 1978) and officially designated as state endangered by the Rhode Island Natural Heritage Program in

1992 (Rhode Island Natural Heritage Program, 1992). *Ophioglossum vulgatum* was listed as threatened in Connecticut in 1991 (Connecticut Department of Environmental Protection, 1991). It has not been granted special status by the other New England states.

This study was undertaken to investigate the ecology, reproductive status and population genetics of *Ophioglossum vulgatum* var. *pseudopodum* and its present distribution in Massachusetts. Specific objectives included (a.) examination of all known populations of *O. vulgatum* in the state, mapping of their distribution and estimation of population sizes; (b.) identification of associated vascular plant species in each site; (c.) analysis of mating systems and assessment of genetic variability for each population through starch gel electrophoresis; (d.) reassessment of the status of *O. vulgatum* in Massachusetts and identification of possible reasons for its apparent success in some locations and its decline in others; and (e.) development of management strategies for preserving the existing populations.

BIOLOGY OF OPHIOGLOSSUM VULGATUM

Gross Morphology, Taxonomy and Distribution

The Ophioglossales have traditionally been considered plants of "ancient lineage and extreme conservatism practically unparalleled in the other fern groups" (Clausen, 1938). Their sporophytes are homosporous, perennial herbs with a single, erect stem bearing one or more small sterile leaves and a single fertile branch with sporangia. The gametophytes are subterranean and nonchlorophyllous (Tryon and Tryon, 1982).

Ophioglossum includes about 30 species grouped in four subgenera and distributed worldwide from the tropics to the Arctic (Tryon and Tryon, 1982). Sporophytes of all *Ophioglossum* species have a short, erect stem 1–12 cm long. The stem bears a single leaf with a mature sterile lamina 1.6–25 cm or more in length. The leaf is usually entire and narrowly elliptic, but in a few species it may be palmately lobed or dichotomously branched. Many species of *Ophioglossum* display reticulate or areolate venation. The fertile branch usually arises at or below the base of the sterile lamina, often in the form of a spike with two rows of large sporangia.

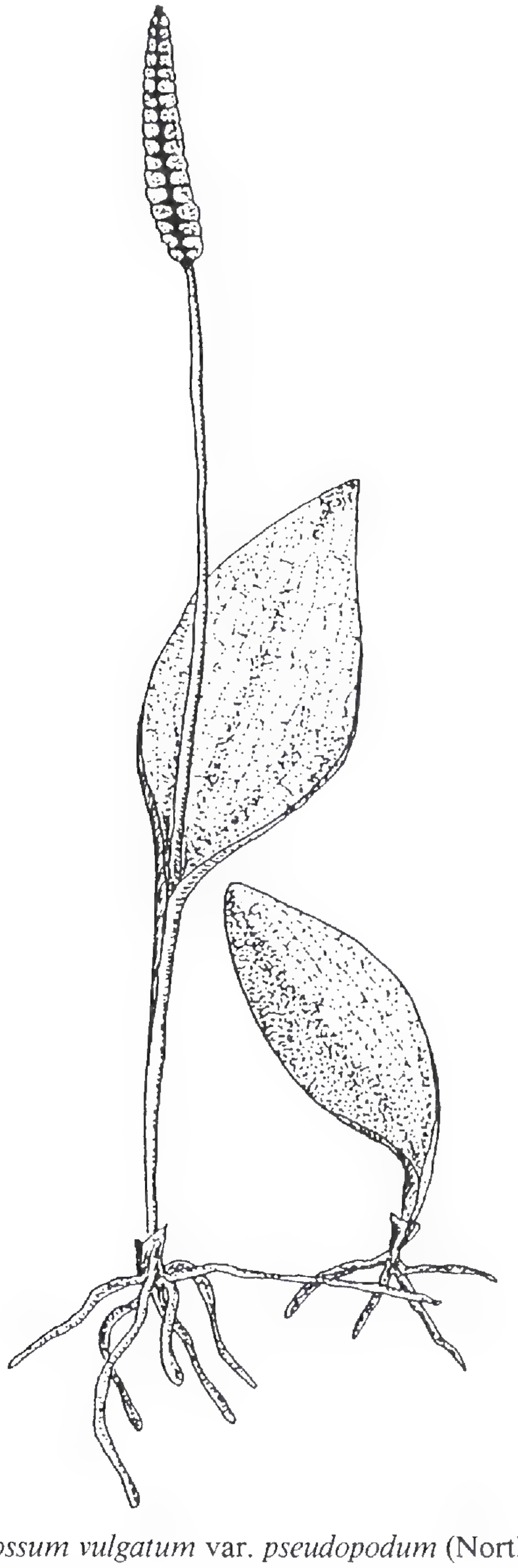

Plate 1. *Ophioglossum vulgatum* var. *pseudopodum* (Northern Adder's-Tongue Fern), natural size. Illustration by Susan Alix Williams, reproduced with the permission of the artist. Originally published in Susan Alix Williams, *Wildflowers of Rowe,* 1991, published by the Rowe Historical Society.

Ophioglossum is characterized by extremely large chromosome numbers. *Ophioglossum reticulatum* L., with n = 631, is believed to possess the largest number of chromosomes of any organism known. Other *Ophioglossum* species range from n = 120 to n = 566 (Tryon and Tryon, 1982).

Ophioglossum vulgatum L. is typical of its genus. The single sterile leaf is elliptic, 2.5–10 cm long and 1–4 cm wide, with a tapered base and reticulate venation. The stalk of the fertile spike is 4–23 cm long with sporangia arranged in two parallel rows 1.5–5 cm long at the tip. From the erect rhizome, numerous slender roots diverge. The gametophyte is subterranean and mycoparasitic (Wagner et al., 1985; Goswami, 1987). The roots of *O. vulgatum*, like those of the other members of the Ophioglossales, are hairless, and some botanists have assumed that mycorrhizae must play an important role in the uptake and transport of water and nutrients (Wagner et al., 1985). Khandelwal (1990) has suggested a chromosome number for *O. vulgatum* of n = 120.

Ophioglossum vulgatum now occurs in North America, Europe, and Asia (Clausen, 1938). This wide range has led botanists to conclude that *O. vulgatum* itself is ancient and was probably widely dispersed in Laurasia before the separation of North America from Eurasia. While it normally occurs at lower elevations, specimens of *O. vulgatum* in the Gray Herbarium have been collected at 4500 feet in Nepal and at 10,000 feet in China.

Fernald (1939) proposed two North American varieties of *Ophioglossum vulgatum*: var. *pseudopodum*, the northern adder's-tongue fern, and var. *pycnostichum*, the southeastern adder's-tongue fern. *Ophioglossum vulgatum* var. *pseudopodum* has a pale green sterile blade that tapers at the base. *Ophioglossum vulgatum* var. *pycnostichum* Fern. is distinguished by its dark green sterile blade with a rounded base (Fernald, 1950). Wagner (1971) believed spore size was another differentiating characteristic of these two varieties, the spores of *O. vulgatum* var. *pseudopodum* averaging 20% larger than those of *O. vulgatum* var. *pycnostichum*. McAlpin (1971) argued that the presence of a persistent sheath in var. *pycnostichum* and its absence in var. *pseudopodum* was an important taxonomic character for distinguishing the two varieties. Lellinger (1985) argued that the two varieties are sufficiently distinct and sufficiently different from *O. vulgatum* L. to justify two separate North American species, *O. pusillum* Raf. and *O. pycnostichum* (Fern.) Löve & Löve. More recently Wagner and Wagner recognized Rafinesque's *O. pusillum* as the northern

form and included *O. pycnostichum* (Fern.) Löve & Löve within the Linnaean *O. vulgatum* (Wagner and Wagner, 1993).

The present study follows the broader and more traditional treatment of *O. vulgatum*. However, all plants investigated represent Rafinesque's *O. pusillum* and Fernald's *O. vulgatum* var. *pseudopodum* (Blake) Farw. and are referred to as *O. vulgatum*.

Life History

Spore Development, Dispersal and Germination

Sori of *Ophioglossum vulgatum* are produced on the single fertile sporophyll with spores maturing in late July or early August in New England. The fully mature sporangia dehisce to release a cloud of yellow, dustlike haploid spores. No estimates have been made of spore production in *O. vulgatum*; however, other ferns with spores of similar size produce between 7.5×10^5 and 7.5×10^9 spores per fertile frond (Page, 1979).

Fern spores are often carried long distances by air currents. However, an increase in atmospheric moisture may result in a sudden, local descent of spores in rainstorms and hence peaks of fern spore deposition may occur during the first rainfall following a warm, dry spell (Page, 1979).

After landing, the spores of *Ophioglossum vulgatum* often percolate several centimeters through porous soil before reaching a stable substrate (Edwards, 1982; Wagner et al., 1985). Germination may commence immediately and proceed rapidly if conditions are suitable; otherwise, development may extend over one or more years (Foster and Gifford, 1974) since prothalli are capable of overwintering (Page, 1979). The spores may also remain dormant for extended periods (Goswami, 1987). When the gametangia mature, motile sperms are released and may move several centimeters either by mass flow of ground water or by flagellar motion (Wagner et al., 1985).

Since the gametophytes of *Ophioglossum* and *Botrychium* lack chloroplasts and grow beneath the soil surface, intragametophytic selfing may be favored because it is unlikely that two spores will land sufficiently near to one another for cross-fertilization to occur and soil particles may impede sperm (Klekowski and Baker, 1966; Tryon and Tryon, 1982; Peck et al., 1990).

Wagner et al. (1985), however, contend that species with subterranean gametophytes may cross-fertilize as frequently as spe-

cies with surficial gametophytes because of the crowding of gametophytes that results when "spore showers" settle out. In addition, herbivores have been observed browsing sporangial clusters and Wagner et al. (1985) hypothesize that spores of *O. vulgatum* may resist digestive processes, be deposited in feces, and germinate in clusters (Wagner et al., 1985).

Nonetheless, isozyme electrophoresis of various *Botrychium* species suggests that intragametophytic selfing predominates (Soltis and Soltis, 1986; McCauley et al., 1985; Watano and Sahashi, 1992).

Vegetative Reproduction

Ophioglossum vulgatum frequently reproduces vegetatively through sporophytes arising directly from the roots of parent plants (Foster and Gifford, 1974). Edwards (1982) studied vegetative growth in a population of *O. vulgatum* in southern England and traced the root system of a single plant for 1.8 m at a depth of 18–25 cm in the soil. Two clonal sporophytes were produced within this distance and the roots may have been connected with other more distant fronds.

Ecology of *Ophioglossum vulgatum*

Ophioglossum vulgatum has been found in such diverse sites as bogs, fens, damp sands, pastures, wet meadows, grassy swales, moist woods, rich swamplands, mud creeks, and cedar swamps. Occasionally it occurs on dry, sandy beaches (Clausen, 1938) or hillsides (SCHN, B. A. Phelps and A. V. Osmun, Cornwall Bridge, CT, 1902) and the subterranean gametophyte may be an adaptation to seasonal drying and/or fire (Wagner et al., 1985).

Overall, *Ophioglossum vulgatum* favors early successional sites (Coddington and Field, 1978; Tryon and Tryon, 1982) and its occurrence often appears to be related to disturbance such as the disruption of soil by grazing herbivores.

METHODS

Herbarium Research and Field Study

In order to determine historical and/or present sites, all Massachusetts specimens of *Ophioglossum vulgatum* were examined

at the Smith College Herbarium (SCHN), the Herbarium of the University of Massachusetts–Amherst (MASS), the Gray Herbarium (GH), the New England Botanical Club Herbarium (NEBC), and the Yale University Herbarium (Y). In addition, the collection records of Harry Ahles and Roberta Poland, both of whom collected extensively in Franklin County, were examined at MASS. The Massachusetts Natural Heritage Program of the Massachusetts Division of Fisheries and Wildlife (MNHP) in Boston also provided records of present and historical populations.

Since 1961, *Ophioglossum vulgatum* has been recorded in Massachusetts at 13 sites. Two sites were not visited due to difficulties in gaining access, although MNHP records indicate that other workers have recently sought *O. vulgatum* at both of these sites without success. The remaining eleven Massachusetts sites were visited between June 1 and August 30, 1992.

At each site where *Ophioglossum vulgatum* was relocated, every sporophyte was flagged and recorded on a detailed site map. The reproductive status of the sporophyte, whether sterile or fertile, was also recorded. Because all populations occurred in open areas surrounded by forest, three species lists were compiled for each site: (1) the dominant trees of the surrounding forest, (2) all vascular plant species in the area where *O. vulgatum* occurred, and (3) associated species, i.e., those within 1 m of any specimens of the population of *O. vulgatum*. Nomenclature of vascular plant species follows Fernald (1950) unless otherwise noted.

Property owners, conservation agents and other researchers were consulted to determine the history of each property, including disturbances caused by beaver occupation, logging, fires, agricultural practices and applications of herbicides.

Laboratory Investigations

Starch gel electrophoresis was carried out on tissue samples from four of the five Massachusetts sites where *Ophioglossum vulgatum* occurred after permission to collect this threatened species was obtained from MNHP. Because of the very small size of its *O. vulgatum* population, no live material was collected at the Brewster site. Because of the large size of the population and the clustered occurrence of the sporophytes at the Conway site, live material was taken from 108 sporophytes, 12 from each of 7 clusters distributed around the site and 24 taken randomly from

around the site. At each of the remaining three Massachusetts field sites, leaf segments were collected from about 12 sporophytes. For purposes of comparison, live material was also obtained from a site at Mt. Sunapee, New Hampshire. Segments ranged from 40 mg to 100 mg depending on the size of the blade. Care was taken not to uproot or otherwise disturb plants from which leaf segments were taken. Each leaf segment was assigned a number and placed in a small plastic bag, its location recorded on a map of the site.

Live material was placed on ice immediately and kept on ice from a few hours to a maximum of five days before processing in the laboratory. Except where noted, the protocol for electrophoresis of ferns by Soltis et al. (1983) was followed.

In the laboratory each specimen was weighed and placed in a mortar chilled in ice. The phosphate grinding buffer-polyvinylpyrrolidone (PVP) solution was prepared in advance except for 2-mercaptoethanol which was added immediately before grinding. The solution was then added to the mortar in the ratio of .4 ml to 100 mg of live material and the mixture ground into a homogenate. Filter paper wicks with dimensions 5 mm × 7 mm were saturated with homogenate, then placed in labeled microtubules. In many instances wicks were utilized immediately. Any wicks held longer than 4 hours were placed at −80°C until immediately before use, a maximum of 15 weeks.

Starch gels with dimensions 13.25 cm × 24.75 cm × 7.5 mm were prepared using 30 g of potato starch (SIGMA S-4501), 50 g of sucrose and 400 ml of gel buffer. Normally, the solution was heated for about 1.5 minutes after reaching the gel point, aspirated for 1 minute, then poured into gel forms, wrapped in plastic wrap, and refrigerated overnight. With gel buffer #6 (Soltis et al., 1983) the solution was heated for 1.75 minutes, then aspirated for 1.5 minutes.

Microtubules containing wicks to be run were thawed in ice water for approximately 15 minutes. Wicks were removed from the microtubule and inserted in one of twenty-four wells along the center of each gel.

Gels were run under refrigeration at approximately 4°C for from 3 to 5 hours with a current between 40 and 65 milliamperes. All enzymes migrated anodally. Two bags of crushed ice and water were placed on top of each gel to prevent overheating and were

changed as needed. When a gel was finished, the power was turned down to 10 milliamperes until ready for slicing. Three to four slices approximately 1.9 mm thick were made from each gel.

One hundred ml of stain was placed on each gel slice which was then kept in the dark at room temperature for from 1 hour to 21 hours depending on the enzyme. Gels were scored and some photographed. Gel slices were then labeled, wrapped in plastic and refrigerated for future reference.

An effort was made to develop a protocol for electrophoresis of *Ophioglossum vulgatum* for each of the following enzymes: Acid phosphatase (APH, EC 3.1.3.2), Aconitase (ACON, EC 4.2.1.3), Aldolase (ALD, EC 4.1.2.13), Aspartate aminotransferase (AAT, EC 2.6.1.1), Catalase (CAT, EC 1.11.1.6), Esterase (EST, EC 3.1.1.–), Fructose-1,6-diphosphatase (F1,6DP, EC 3.1.3.11), Glutamate dehydrogenase (GDH, EC 1.4.1.2), Glucose-6-phosphate dehydrogenase (G6PD, EC 1.1.1.49), Glyceraldehyde-3-phosphate dehydrogenase (G3PD, EC 1.2.1.12), Hexokinase (HK, EC 2.7.1.1), Isocitrate dehydrogenase (IDH, EC 1.1.1.42), Malate dehydrogenase (MDH, EC 1.1.1.37), Malic enzyme (ME, EC 1.1.1.40), 6-Phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44), Phosphoglucoisomerase (PGI, EC 5.3.1.9), Phosphoglucomutase (PGM, EC 2.7.5.1), Shikimate dehydrogenase (SkDH, EC 1.1.1.25), and Triosephosphate isomerase (TPI, EC 5.3.1.1).

Protocols were developed that produced observable bands for ten enzymes and 26 loci:

1. Acid phosphatase (APH-1, APH-2, APH-3)
2. Esterase (EST-1, EST-2, EST-3)
3. Glucose-6-phosphate dehydrogenase (G6PD-1, G6PD-2, G6PD-3)
4. Isocitrate dehydrogenase (IDH)
5. Malate dehydrogenase (MDH-1, MDH-2, MDH-3)
6. Malic enzyme (ME-1, ME-2, ME-3)
7. 6-Phosphogluconate dehydrogenase (6PGD-1, 6PGD-2)
8. Phosphoglucoisomerase (PGI-1, PGI-2)
9. Phosphoglucomutase (PGM-1, PGM-2)
10. Triosephosphate isomerase (TPI-1, TPI-2, TPI-3, TPI-4).

For G6PD, IDH, MDH, 6PGD and PGM, buffer system 2 was utilized. For APH and ME, buffer system 6 was used. For EST,

PGI and TPI, buffer system 8 was used. When more than one locus was observed for an enzyme, loci were numbered with the locus migrating farthest identified as number 1.

A set of gels was run for each of the seven clusters of sporophytes in the Conway site in order to assess genetic variability within clusters. Another set of gels was then run with one or two specimens from each of the seven Conway clusters to assess variability between clusters. A third set of gels was run using twelve sporophytes from around the Conway site outside of the clusters already sampled. A fourth set of gels was run for each of the other five populations using a Conway specimen as a standard. Finally, a set of gels was run with representatives of each of the populations to assess variation between populations. Included on this final gel were specimens of a tropical species, *Ophioglossum reticulatum*, obtained from the Lyman Plant House at Smith College, and specimens of *Botrychium dissectum* and *B. dissectum* var. *obliquum* obtained from a local woodland. The same Conway specimen was used as a standard.

RESULTS AND DISCUSSION

Ophioglossum vulgatum in Massachusetts: Historical Status

The earliest reference to *Ophioglossum vulgatum* in Massachusetts appears in Josselyn's *New England's Rarities* (1672), where the species is reported to occur "upon dry hill grounds [and] in places where the water hath flood all Winter. . . ."

Ophioglossum vulgatum is listed in Hitchcock's *Catalogue of Plants Growing Without Cultivation in the Vicinity of Amherst College* (1829) and in the first complete flora of Massachusetts (Hitchcock, 1833) with a location "in the vicinity of Amherst."

MNHP lists 105 current or historical records for *Ophioglossum vulgatum*. Collection dates range from 1848 to 1991 from 89 cities and towns in all 14 counties (Figure 1). The five herbaria consulted for this project contain 101 dated Massachusetts specimens from 70 cities and towns in all 14 counties. Collection dates range from 1848 to 1986. *Ophioglossum vulgatum* was most widely distributed in Massachusetts from 1870 to 1939 and more widely collected in western Massachusetts (Table 1). Collections in eastern Massachusetts peaked during the period 1870 to 1919. Only five

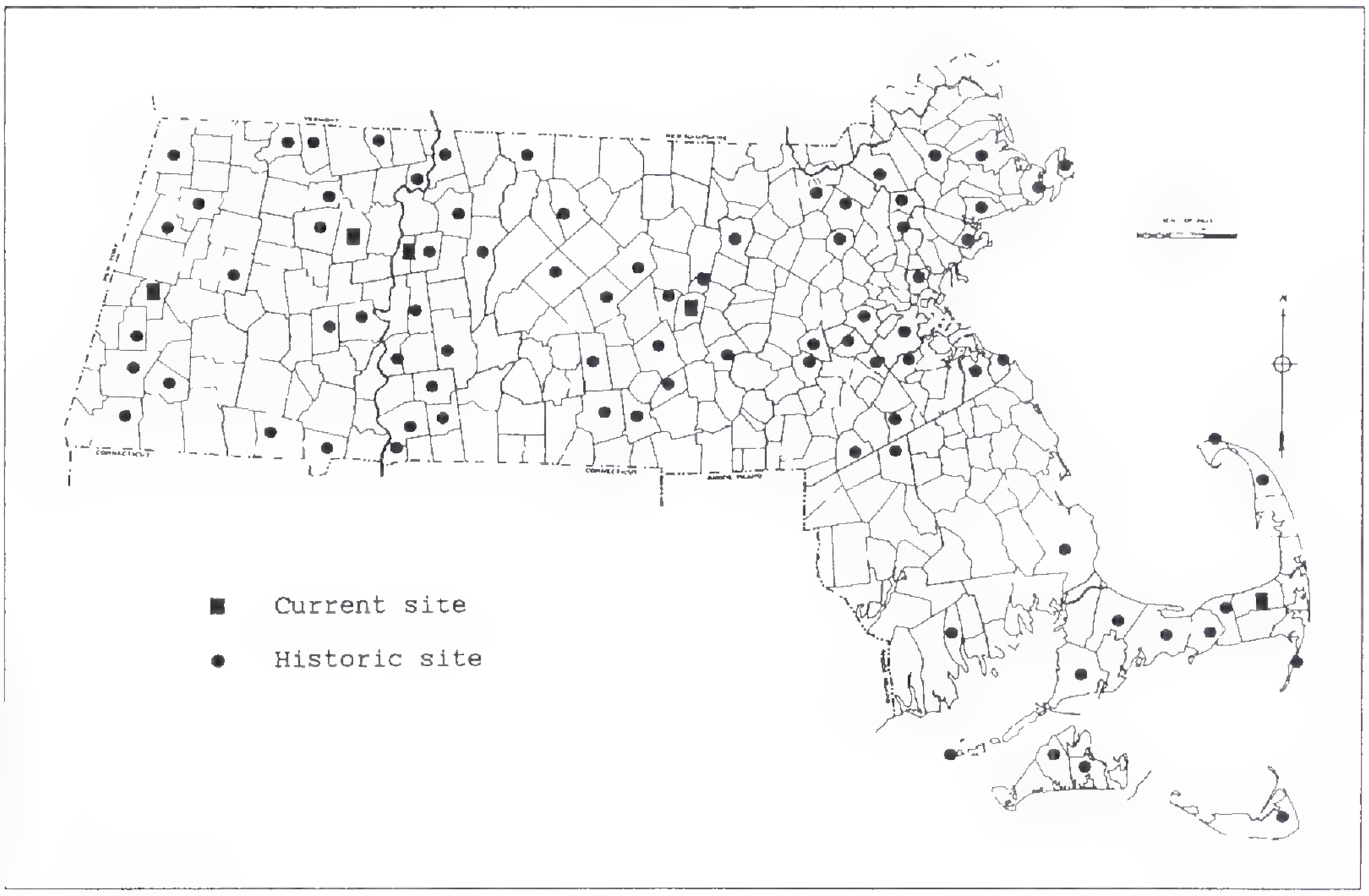

Figure 1. Current distribution and recorded historical sites of *Ophioglossum vulgatum* by city or town in Massachusetts.

specimens have been collected east of Worcester County since 1919. No more than 14 collections exist for any decade and in some decades *O. vulgatum* has not been collected at all.

Coddington and Field (1978) considered *Ophioglossum vulgatum* widespread but rare in Massachusetts and recommended its inclusion in a proposed list of rare and endangered plant species for the state, noting ". . . few field botanists have seen it. Characteristic of early successional habitats." Massachusetts collections of *O. vulgatum* range from sea level to 1200 feet, in habitats ranging from bogs, abandoned beaver meadows and pastures to old fields and power line rights-of-way.

Field Sites and Population Histories

Current Sites in Massachusetts

Five populations of *Ophioglossum vulgatum* were relocated, one each in Conway and Sunderland (Franklin County), Lenox (Berkshire County), Boylston (Worcester County), and Brewster (Barnstable County).

Conway, MA. The Conway, MA site is located northwest of Conway State Forest in Franklin County. It occupies .96 ha at an

Table 1. Dated records of *Ophioglossum vulgatum* from Mass. Natural Heritage Program; records for eastern and western Massachusetts grouped by decade. Eastern Massachusetts includes Essex, Middlesex, Suffolk, Norfolk, Bristol, Plymouth, Barnstable, Dukes and Nantucket Counties. Western Massachusetts includes Berkshire, Hampden, Hampshire, Franklin and Worcester Counties.

Time Period	Eastern Mass.	Western Mass.	Total
1840–1849	0	1	1
1850–1859	0	0	0
1860–1869	0	2	2
1870–1879	9	5	14
1880–1889	9	4	13
1890–1899	2	1	3
1900–1909	5	7	12
1910–1919	10	4	14
1920–1929	2	12	14
1930–1939	0	9	9
1940–1949	0	1	1
1950–1959	0	0	0
1960–1969	1	1	2
1970–1979	1	2	3
1980–1989	1	2	3
1990–present	0	0	0
Total	40	51	91

elevation of 450 m above sea level and slopes gently from southwest to northeast.

Aerial photographs indicate that low shrub vegetation covered the site in 1952 and 1958. Beavers were active in the area in the early 1960's (C. J. Burk, pers. comm.) and by the mid-1960's the site was covered with water to a depth of over 1 m. The pond was abandoned in the late 1960's, probably as a result of trapping. Aerial photographs taken in 1971 show that half of the site was covered with open water and the rest with grass and sedge vegetation. By July, 1980, the open water occurred only in front of the dam (Mosher, 1981). Standing water now covers much of the site at frequent intervals during the growing season.

Dominants of the surrounding forest are typical components of the northern hemlock-hardwood forest including *Acer saccharum, Betula lutea, Fagus grandifolia, Pinus strobus* and *Tsuga canadensis.*

The current Conway population was first discovered by Nancy D. Mosher (Nancy D. McMaster) in 1980 (Mosher, 1981) and

Plate 2. Abandoned beaver meadow in Conway (Franklin County), MA, an open marsh dominated by *Typha latifolia, Spiraea latifolia* and *S. tomentosa* and a current site for *Ophioglossum vulgatum.*

reported to MNHP in 1985. In July, 1980, when the vegetation in the site was first sampled, 26 sporophytes of *Ophioglossum vulgatum* were present (Mosher, 1981). Approximately 40 sporophytes of *O. vulgatum* were found in the site in 1985 (N. McMaster, 1989) and approximately 50 in 1990 (N. McMaster, 1990, unpubl. data). By July, 1991, the population had increased sharply to a total of 901 sporophytes (R. McMaster, 1991), and by August and September, 1992, had declined slightly to 866 sporophytes.

Most sporophytes in 1991 occurred in clusters of 10–27 stems. Clusters were roughly circular with a radius of about .5 m. Frequently, clusters grew on patches of somewhat elevated substrate, either around the bases of shrubs such as *Alnus rugosa, Salix* spp., or *Spiraea* spp., or on submerged logs covered with bryophytes in the wetter soils of depressions. A few clusters occurred in lower areas, however, and some sporophytes were not clustered, with individual stems occurring .5 m or more from the nearest member of the population. An estimated 61% of the sporophytes were fertile (R. McMaster, 1991).

Ophioglossum vulgatum was not found where open water or mud was present, nor in drier areas around the margins where trees and shrubs predominated. Its frequency decreased abruptly

on the southwestern edge of the site which supported a dense cover of sedges and grasses.

In the immediate vicinity of the *Ophioglossum vulgatum* population, associated shrubs and small trees included *Acer rubrum, Alnus rugosa, Betula populifolia, Pinus strobus, Salix discolor, S. sericea, Spiraea latifolia* and *S. tomentosa.* Associated herbaceous species in the immediate vicinity included *Carex lurida, Drosera rotundifolia, Dulichium arundinaceum, Eleocharis tenuis, Epilobium strictum, Equisetum arvense, Eupatorium maculatum, E. perfoliatum, Galium tinctorium, Glyceria canadensis, Hydrocotyle americana, Hypericum virginicum, Impatiens capensis, Juncus effusus, Juncus* sp., *Leersia oryzoides, Liparis loeselii, Lycopus virginicus, Mentha arvensis, Muhlenbergia mexicana, Onoclea sensibilis, Osmunda regalis, Polygonum sagittatum, Sagittaria latifolia, Scirpus cyperinus, Solidago canadensis, S. graminifolia, Sparganium americanum, Thelypteris palustris* Schott, *Typha latifolia,* and *Viola pallens* (McMaster, 1991).

Sunderland, MA. The Sunderland, MA (Franklin County) site is located in an electrical transmission line right-of-way at an elevation of 220 m. The site slopes gradually from east to west and is seasonally wet.

The right-of-way was established in about 1912 and is maintained by cutting, pruning and periodic chemical treatment of any trees or shrubs that might interfere with the operation of the transmission lines. The site was last cut back or treated in 1989 (R. Farrell, pers. comm.).

On both sides the site adjoins northern hardwood forest dominated by *Acer saccharum, Betula papyrifera, B. populifolia, Carya ovata, Pinus strobus,* and *Quercus rubra.*

The population of *Ophioglossum vulgatum* was first reported in 1986 by Bruce Sorrie of the MNHP and Robert Ruhful of the University of Massachusetts–Amherst. A total of 80 plants of *O. vulgatum* were located over a .4–.8 hectare area.

At this site in August, 1992, the population of *Ophioglossum vulgatum* had decreased to 21 sporophytes occurring throughout a roughly rectangular area 8 m × 2 m. There were only 2 fertile sporophytes. Most leaf blades were small with atypically brown or yellow patches. Associated shrubs and small trees in the immediate vicinity included *Acer rubrum, Betula lenta, Cornus racemosa, Hamamelis virginiana, Lindera benzoin, Lyonia ligustrina, Rubus* sp. and *Salix* sp. Associated herbaceous species

included *Achillea millefolium, Carex scoparia, C. stipata, Cirsium arvense, Equisetum sylvaticum, Fragaria virginiana, Galium asprellum, Geranium maculatum, Hypericum ellipticum, Juncus effusus, Onoclea sensibilis, Osmunda cinnamomea, Platanthera flava* (L.) Lindl., *Polygonum sagittatum, Prunella vulgaris, Solidago graminifolia, Thelypteris palustris,* and *Viola* spp.

Lenox, MA. The Lenox, MA (Berkshire County) site is located on the edge of an open meadow at an elevation of 370 m. The seasonally wet site slopes gently from west to east and has been described as a "sloping graminoid fen" (P. Weatherbee, pers. comm.).

The area was used for pasture until 1939 and aerial photographs show it has been kept open, probably by mowing or haying, since. During the 1980's a stream to the west was dammed by beavers, causing surface water to flow across the site, which was last mowed in 1989 (P. Weatherbee, pers. comm.).

The forest surrounding the meadow is dominated by *Acer rubrum, A. saccharum, Carya ovata, Malus* sp., *Pinus strobus* and *Populus tremuloides* with an understory of *Betula papyrifera, Fraxinus americana, Prunus virginiana,* and *Viburnum recognitum. Celastrus orbiculatus* and *Vitis* spp. frequently overtop the canopy to the west. *Alnus* sp. dominates the wetter eastern boundary of the meadow.

The population of *Ophioglossum vulgatum* was discovered and reported to MNHP by Pamela B. Weatherbee in 1991. A total of 205 sporophytes occurred in a roughly rectangular area measuring 11 m × 26 m. Twenty-two percent of the sporophytes were fertile.

Within this area in August, 1992, the population of *Ophioglossum vulgatum* had declined to 62 sporophytes. Approximately 33% of these were fertile. Most were growing beneath low shrubs, either *Cornus stolonifera, Salix serissima* or *Salix discolor.* Other associated species in the shrub layer included *Potentilla fruticosa, Viburnum recognitum, Rhamnus cathartica, Salix serissima, S. discolor* and *Vitis* sp. Herbaceous species included *Achillea millefolium, Carex stricta* var. *strictior, Equisetum arvense, Eupatorium maculatum, Festuca* sp., *Fragaria virginiana, Galium triflorum, Geum rivale, Juncus canadensis, J. dudleyi, Lysimachia ciliata, Onoclea sensibilis, Parthenocissus quinquefolia, Phleum pratense, Prunella vulgaris, Rudbeckia hirta, Scirpus atrovirens, Spiraea latifolia, Thelypteris palustris, Trifolium repens, T. agrarium,* and *Valeriana officinalis.*

Plate 3. Two sporophytes of *Ophioglossum vulgatum,* one with sporophyll, in Lenox (Berkshire County), MA.

Boylston, MA. The Boylston, MA (Worcester County) site is located at the eastern edge of a meadow which slopes from west to east at an elevation of 170 m. Occasionally, shallow standing water occurs on the lowest part of the meadow about 50 m north of the site (J. Wright, pers. comm.).

The site was used for pasture before 1986. The meadow was cut for hay in 1986 and 1987 and mowed once a year in October in 1988, 1989, 1990 and 1992.

The adjacent forest includes a canopy of *Acer rubrum, Carya* sp., *Fraxinus americana, Malus* sp., *Pinus strobus, Prunus serotina* and *Quercus velutina* and an understory of *Prunus virginiana* and *Rhamnus frangula.*

Shrubs and small trees found in the adjacent upland meadow include *Acer rubrum, Cornus amomum, Prunus serotina, Rhamnus frangula, Salix bebbiana, Spiraea latifolia, S. tomentosa,* and *Viburnum recognitum.* Herbaceous species of the upland meadow include *Daucus carota, Eupatorium maculatum, Galium tinctorium, Onoclea sensibilis, Rhus radicans, Rosa nitida, Solidago canadensis, S. rugosa, Trifolium hybridum, T. pratense, Vicia cracca* and *Vitis labrusca.*

The "very vigorous" population of *Ophioglossum vulgatum* consisted of 30–40 plants when first reported in 1989 by Marc Larocque. When the population was surveyed in August, 1992, it had increased to 109 sporophytes located in a level area about 12 m × 20 m. However, only 18% of the sporophytes were fertile. Many sporophytes occurred beneath shrubs of *Cornus amomum* and *Salix* spp. between .3 m and 1.0 m high. Associated shrubs and tree seedlings included *Acer rubrum, Alnus rugosa, Betula populifolia, Cornus amomum, Malus* sp., *Prunus serotina, Quercus rubra, Rhamnus frangula, Rhus radicans, Rosa nitida, Spiraea latifolia, S. tomentosa, Vaccinium corymbosum,* and *Viburnum recognitum.* Herbaceous species included *Achillea millefolium, Agrostis stolonifera, Asclepias syriaca, Asparagus officinalis, Carex stricta, Daucus carota, Galium tinctorium, Onoclea sensibilis, Osmunda regalis, Oxalis montana, Solidago canadensis, S. gigantea, S. rugosa, Trifolium hybrida, T. pratense, Rubus* sp., and *Vicia cracca.*

Brewster, MA. The Brewster, MA (Barnstable County) site is located in a small clearing adjacent to a pond at an elevation of 8 m. The site is seasonally wet and was probably kept clear by

periodic mowing until 1985. There has been no clearing since 1985 (R. Finch, pers. comm.).

The adjacent woodland is dominated by *Acer rubrum* and *Nyssa sylvatica.*

The population of *Ophioglossum vulgatum* included 19 plants when first reported by Richard LeBlond in 1985. Mario Di-Gregorio, then Conservation Agent for the Town of Brewster, observed the population from 1986 to 1989 and reported finding six sterile plants and four to five fertile plants each year. He had been unable to relocate any plants since 1989.

In July, 1992, only a single sterile sporophyte was located. Associated shrubs and small trees included *Acer rubrum, Leucothoë racemosa, Lyonia ligustrina, Nyssa sylvatica, Rhododendron viscosum, Vaccinium corymbosum* and *V. macrocarpon.* Herbaceous species included *Maianthemum canadense, Rubus hispidus,* and *Trientalis borealis.* Extensive areas were covered by *Sphagnum* spp. and other mosses.

Recent Historical Sites in Massachusetts

Six historical Massachusetts sites were visited but no population of *Ophioglossum vulgatum* found. These occurred at Lanesboro (Berkshire County), Rowe and Gill (Franklin County), Northampton (Hampshire County), Plymouth (Plymouth County), and Falmouth (Barnstable County).

Lanesboro, MA. The Lanesboro, MA population of *Ophioglossum vulgatum* was located by Pamela B. Weatherbee in 1984 when 15 sterile and 3 fertile sporophytes were found at the eastern base of an outcrop of rock in an old field, an area underlain by limestone. No sporophytes have been found on the site since 1984 (P. Weatherbee, pers. comm.).

Rowe, MA. The Rowe, MA population was located by Nancy Williams and Susan Williams in 1983 when approximately 150 sporophytes were found in a "borrow pit." In 1973 sand and gravel were removed from the site which was subsequently colonized by herbaceous vegetation, small shrubs and tree seedlings. The population of *Ophioglossum vulgatum* was seen yearly from 1983 to 1988 but not since in spite of repeated observations of the area (N. Williams, pers. comm.).

Gill, MA. The Gill, MA population was found in 1961 in a "marshy field." I was unable to relocate the population in June,

1992. The wet meadow apparently had been disturbed recently by mowing and excavation.

Northampton, MA. The Northampton, MA population was located by Harry Ahles in 1978 in what was described as a wet hay field. Bruce Sorrie searched unsuccessfully for the population in 1986. I was unable to relocate the population in July, 1992.

Plymouth, MA. The Plymouth, MA population was located by Bruce Sorrie in 1983 in an acid seep. I was unable to relocate the population in June, 1992.

Falmouth, MA. The Falmouth, MA population was located by H. K. Svenson in 1971 in the bottom of a glacial kettle near the town landfill. The site was apparently destroyed in the expansion of the landfill and my efforts to relocate the population in June, 1991 were unsuccessful.

1993 Observations

All four western Massachusetts populations of *Ophioglossum vulgatum* that were extant in 1992 were monitored during the hot, dry summer of 1993. The Conway population was thriving throughout the summer of 1993. Stem counts in eight permanent plots showed a 64% increase over similar counts made in 1991. The Sunderland population had dwindled to one small, withered blade when observed on August 5, 1993. No sporophytes of the Lenox population were in evidence on July 24, 1993. Some sporophytes of the Boylston population were observed to be in good condition in early July, 1993, but had died back by August 18, 1993 (J. Wright, pers. comm.).

Laboratory Investigations

A total of 157 individuals of *Ophioglossum vulgatum* was assayed at 26 loci (Table 2). All individuals in all populations were found to be homozygous and monomorphic for all observable loci.

Additional confirmation of the observed monomorphism among the specimens assayed was obtained by electrophorescing material from all five populations of *Ophioglossum vulgatum* (four from Massachusetts, one from New Hampshire) with material of *O. reticulatum, Botrychium dissectum* and *B. dissectum* var. *obliquum* on a single gel. Results for the three New Hampshire spec-

Table 2. Total sample size and number of specimens for which satisfactory band resolution was achieved at each locus in each site, CONway, SUNderland, LENox, BOYlston and MT. Sunapee. (—) indicates unsatisfactory band resolution.

Locus	CON	SUN	LEN	BOY	MTS	TOTAL
Total sample size	108	13	11	13	12	157
APH-1	59	—	—	—	—	59
APH-2	33	—	—	—	—	33
APH-3	24	—	—	—	—	24
EST-1	16	—	—	—	—	16
EST-2	12	—	—	—	—	12
EST-3	12	—	—	—	—	12
G6PD-1	59	7	7	11	1	85
G6PD-2	52	—	—	—	—	52
G6PD-3	16	—	—	—	—	16
IDH	75	13	11	1	12	115
MDH-1	85	13	11	11	8	128
MDH-2	79	12	11	11	3	116
MDH-3	21	—	—	—	—	21
ME-1	85	13	5	1	—	104
ME-2	38	13	5	1	—	57
ME-3	1	1	5	3	—	10
PGI-1	93	13	11	11	12	140
PGI-2	69	13	11	10	12	115
PGM-1	77	13	11	13	8	122
PGM-2	29	—	—	—	—	29
6PGD-1	72	—	3	—	—	75
6PGD-2	50	—	—	—	—	50
TPI-1	39	1	11	1	7	59
TPI-2	22	1	11	2	7	43
TPI-3	19	1	7	—	7	34
TPI-4	6	—	—	—	7	13

imens of *O. vulgatum* were inconclusive and warrant additional study. Bandings for *O. reticulatum, B. dissectum* and *B. dissectum* var. *obliquum* were distinct from each other and from *O. vulgatum.*

The number of loci assayed represents only a small portion of the total genome of *Ophioglossum vulgatum.* The significance of complete monomorphism for these loci, however, is enhanced by the fact that the same 26 loci found to be monomorphic for specimens of *O. vulgatum* have been widely assayed for other homosporous ferns and frequently have been observed to be polymorphic (McCauley et al., 1985; Soltis and Soltis, 1986; Soltis and Soltis, 1988; Watano and Sahashi, 1992). No other published data on genetic variation in *Ophioglossum vulgatum* was found.

Lack of genetic variability often has been cited as a factor in the decline in population size and, in some cases, in the extinction of rare plant species (Frankel and Soulé, 1981; Simberloff, 1986; Barrett and Kohn, 1991; Huenneke, 1991). Data from the electrophoresis of specimens from four of the Massachusetts populations of *Ophioglossum vulgatum* show a complete absence of genetic variability at all loci assayed. Any explanation for this observation must account for three phenomena: (1) the apparent lack of genetic variability within sporophytes; (2) the apparent lack of genetic variability among individuals within each population; and (3) the apparent lack of genetic variability among populations.

If intragametophytic selfing occurs, all heterozygosity will be lost in one generation but there still may be some differentiation within a population. Reductions in genetic variability may also occur as a result of small effective population size. Decline in effective population size may result when few individuals reproduce, when the number of progeny produced by individuals varies widely, and/or when a population bottleneck, an extreme reduction in effective population size, occurs resulting in the transmission of only a small subset of the total genetic variability of the population to the next generation (Frankel and Soulé, 1981). A population with a small effective population size is also susceptible to further loss of alleles due to genetic drift. Edwards (1982) observed a population of *Ophioglossum vulgatum* in southern England, for example, in which only 1–2% of the sporophytes bore fertile fronds. Similarly, in the Sunderland population less than 10% of the sporophytes found in the summer of 1992 had fertile fronds. In addition, populations of clonal species such as *O. vulgatum* may contain numerous sporophytes of a single genotype.

New populations established by dispersal of spores from a genetically monomorphic population will normally be of the same homozygous genotype. If the species is capable of rapid vegetative growth, it is possible for a number of large, homozygous, monomorphic populations to develop in a relatively short period of time.

One adaptive compensation for the loss of genetic variation in a population may be the purging of deleterious recessive alleles through repeated episodes of in-breeding (Frankel and Soulé, 1981; Lesica and Allendorf, 1992). By this mechanism, a predominantly self-fertilizing species such as *Ophioglossum vulgatum* character-

ized by low genetic variability may have evolved a complex of alleles co-adapted to a very specific set of environmental conditions. While it is unable to adapt successfully to changes in those conditions, it is suited to sites where those conditions prevail.

The four western Massachusetts populations may have arisen from a single monomorphic population. Gene flow from genetically distinct populations apparently has not occurred or has occurred at sufficiently low frequencies that any variability introduced has been lost through repeated intragametophytic selfing, population bottlenecks and drift. Electrophoretic analysis of populations of *Ophioglossum vulgatum* in neighboring states could shed additional light on these questions.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The five current Massachusetts sites for *Ophioglossum vulgatum* vary significantly in geography, climate, soil and surrounding forest type, but share three important characteristics:

(1) Each site has a history of disturbance that has reduced competition from shrubs and small trees. The Conway site was occupied by beavers. The Sunderland site has been subject to periodic pruning or application of herbicide for maintenance of the power line right-of-way. The Lenox site was occupied by beavers and has been mowed occasionally. The Boylston site was formerly pasture and has been mowed or hayed regularly for many years. The Brewster site was probably maintained irregularly as a lawn.

(2) Each site is characterized by wet conditions for at least a part of the year. The Conway site is saturated throughout the growing season with standing water at frequent intervals. The Sunderland, Lenox, Boylston, and Brewster sites are subject to seasonal flooding, usually in spring and fall.

(3) Each site supports a characteristic flora. Although no single plant species occurs with *Ophioglossum vulgatum* in all five sites, *Acer rubrum* and *Onoclea sensibilis* are abundant in four of the sites and *Achillea millefolium, Spiraea latifolia* and *Thelypteris palustris,* are abundant in three of the sites. Sporophytes of *O. vulgatum* often are found growing in the shade of small shrubs, usually *Alnus* spp., *Cornus* spp., *Salix* spp., or *Spiraea* spp. In the Brewster site the single *O. vulgatum* sporophyte occurred beneath *Leucothoë racemosa.*

Observation of populations over several growing seasons suggest that where the shrub layer is completely lacking, aggressive grass, sedge and rush species predominate and *Ophioglossum vulgatum* declines. The shrub layer, when present, may help to control competition from those species. *Ophioglossum vulgatum* seems to prefer sites where the shrub layer is present but constrained by pruning or periodic flooding.

Populations of *Ophioglossum vulgatum* are capable of sudden and dramatic increases or declines. The current Conway site appears to have increased from 26 sporophytes in 1980 to a maximum of 901 in 1991, the Lenox site from 0 to 205 in under 12 years, and the Boylston site from 30 or 40 to 109 in three years. Conversely, the Rowe population of approximately 150 sporophytes disappeared completely after the 1988 growing season and the Brewster population of 19 in 1985 had declined to only one in 1992. Five additional more gradual extinctions have been documented in the state since 1961.

The low levels of genetic variability revealed by electrophoresis may be important factors in the decline of *Ophioglossum vulgatum* in Massachusetts. A combination of intragametophytic selfing, small population size, low numbers of reproductively mature sporophytes, founder effect and specialized habitat requirements may be responsible for the loss of genetic variability within and among populations. These processes may in turn lead to an inability to adapt to environmental change in an inherently volatile habitat. While *O. vulgatum* seems to be well adapted to compete in early successional sites in Massachusetts, it may lack the genetic heterogeneity that would allow it to persist as these sites change. Only at the Conway site where succession is inhibited by intermittent flooding does *O. vulgatum* appear to thrive. Hence its long-term survival in Massachusetts may be a function not of adaptation to changing conditions in a site, but of its ability to disperse to new, sometimes distant sites and to found new populations successfully.

The habitat requirements and reproductive biology of *Ophioglossum vulgatum* described suggest a number of measures for the management of existing populations.

(1) Plant species competing with *Ophioglossum vulgatum* should be controlled. Shrubs and small trees in the immediate vicinity should be selectively pruned to provide moderate levels of filtered light. The surrounding forest canopy may also require periodic

thinning. Because the effects of herbicides on *O. vulgatum* are not known, their use to suppress surrounding vegetation is not recommended. However, most populations of *O. vulgatum* are small enough that competing vegetation can be controlled by mechanical means such as a portable "weed-wacker" or even hand clippers. The invasion of grasses, sedges and rushes may be restricted by mowing late in the growing season, probably after October 1. Care should be taken to protect shrubs and small trees from damage during mowing.

(2) Disruption or compaction of soil should be avoided. Heavy mowing equipment should not be used to clear *Ophioglossum vulgatum* sites. Footpaths and vehicle rights-of-way should be diverted to provide a generous buffer zone around protected populations.

(3) Proper hydrological conditions in the immediate vicinity of the *Ophioglossum vulgatum* population should be maintained. Extended inundation or desiccation of the substrate during the growing season which may result from beaver activity or anthropogenic activities such as draining and filling often associated with agriculture and highway construction should be avoided.

The size of an *Ophioglossum vulgatum* population may fluctuate dramatically from year to year depending on availability of light, soil moisture, disturbance and other conditions. Because of the extensive root network and the ability of a population to expand vegetatively, it may also be important to protect and manage a site even after all sporophytes have disappeared. It is possible that a subsequent reversal of environmental conditions could result in the development of new sporophytes from the dormant root system. Germination of spores or gametophytes may also occur after an extended period of dormancy.

Habitat for *Ophioglossum vulgatum* also may be provided in sites where it does not occur at present, particularly when those sites are near existing populations. Minimum requisite conditions should include a saturated substrate and moderate to high light levels. Sites where such conditions occur naturally may include seeps, wet meadows and abandoned beaver meadows. Areas subject to some human disturbance also may be appropriate including highway shoulders or median strips, golf courses, utility corridors, or pastures.

While historical data suggest that *Ophioglossum vulgatum* has never been abundant in Massachusetts, its present status is pre-

carious. Of the five known populations, the Brewster population with its single sporophyte is probably destined for extinction, while the Boylston, Lenox and Sunderland populations are marginal. The Conway population, while relatively large and healthy in 1991 and 1992, could easily be subject to the kind of sudden decline that has been observed at other sites.

Continued availability of disturbed, early successional sites may be important to the survival of *Ophioglossum vulgatum* in Massachusetts. These sites may result from naturally occurring disturbances such as wildfires, windstorms, debris slides and insect predation. Some anthropogenic factors such as highway and dam construction may favor the creation of disturbed sites while others, such as the decline of agriculture and suppression of wildfires, may result in less disturbance. While the reintroduction of beavers into the state in the 1930's created new early successional sites, the subsequent expansion of beaver populations may have had the opposite effect, forcing beavers to reoccupy abandoned sites before early successional species were able to colonize them. Thus human activity can be either beneficial or harmful to the survival of *O. vulgatum* in Massachusetts.

Efforts should be made to locate additional populations of *Ophioglossum vulgatum* in Massachusetts. Hagenah (1966) writes "[*Ophioglossum vulgatum*] blends with the grasses and other vegetation, but after the first one is noticed search may reveal scores or even hundreds more." Similarly, Wagner (1971) observes that "Many botanists and naturalists regard the adder's-tongue as a rare plant, but this is probably due largely to the fact that it is overlooked." Roberta Poland (MASS) located at least 11 stations for *O. vulgatum* in the town of Deerfield alone during the 1950's, an achievement which should inspire continued persistence in the search for this ancient and intriguing plant.

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DEPARTMENT OF BIOLOGICAL SCIENCES
SMITH COLLEGE
NORTHAMPTON, MA 01060

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A NEW TRI-HYBRID LYCOPOD, *DIPHASIASTRUM DIGITATUM* × *SABINIFOLIUM*

ARTHUR V. GILMAN

ABSTRACT

A putative tri-specific hybrid *Diphasiastrum* (Lycopodiaceae) is described from a collection in northern Vermont and is figured in a line drawing. The hybrid is morphologically intermediate between its probable parents, *D. digitatum* and *D.* ×*sabinifolium*. This is the first flat-branched hybrid lycopod believed to involve three parental genomes. In light of its limited occurrence (a single clone), it is not given an epithet.

Key Words: *Diphasiastrum* (*Lycopodium*), hybrid, genome analysis, species concept, Vermont

INTRODUCTION

Five species, and at least five hybrids, of the "flat-branched" lycopods (*Diphasiastrum* Holub) are known in northeastern North America (Table 1). The taxonomy of this group has to date relied almost entirely on morphology. Hybrids generally display characters intermediate between their parents, and are usually distinguishable in the field and herbarium on morphological grounds (Wilce, 1965). Cytological work has indicated that all North American species and hybrids share a chromosome number 2n = 46 (F. S. Wagner, 1992), with apparent normal pairing behavior and spore formation in the hybrids (the plant described here produces well-formed spores). Additionally, the difficulty of germinating spores *in vitro* and growing the resulting plants has so far precluded artificial crossing experiments in *Diphasiastrum,* and the genus as a whole has not been analyzed on the basis of isozymes or DNA. On morphological grounds, Wilce (1965) determined *D.* ×*sabinifolium,* which had long been considered a species, to be the hybrid *D. sitchense* × *tristachyum,* a treatment which has gained acceptance (Beitel, 1979; Cody and Britton, 1989; Wagner and Beitel, 1993). Except for *D.* ×*issleri,* which is known in our area from a single collection, and *D. complanatum* × *digitatum,* which may be quite rare, the hybrids are sometimes locally common (Cody and Britton, 1989; W. H. Wagner, pers. comm.), and *D.* ×*sabinifolium* sufficiently so to be regarded as a nothospecies. The hybrids appear to be fertile (F. S. Wagner, 1992), yet no hybrid progeny or backcrosses with parent species

Table 1. Species and hybrids of *Diphiastrum* in northeastern North America (all 2n = 46).

Species
D. digitatum (Dill.) Holub
D. complanatum (L.) Holub
D. tristachyum (Pursh) Holub
D. sitchense (Rupr.) Holub
D. alpinum (L.) Holub
Hybrids
D. ×*sabinifolium* (Willd.) Holub (*sitchense* × *tristachyum*)
D. ×*habereri* (House) Holub (*digitatum* × *tristachyum*)
D. complanatum × *digitatum*
D. ×*zeilleri* (Rouy) Holub (*complanatum* × *tristachyum*)
D. ×*issleri* (Rouy) Holub (*alpinum* × *tristachyum*)

have been described. This paper discusses a new hybrid, *D. digitatum* × *sabinifolium*, at present known from a single station in northern Vermont. It is the first hybrid known to have a hybrid parent.

HYBRID DESCRIPTION AND ANALYSIS

While collecting a series of pteridophytes in Caledonia County, Vermont, I discovered, in a montane (ca. 540 m) east-facing pasture, an unusual clone of *Diphasiastrum* which was not readily referable to any described taxon. It was growing with *D. digitatum* and *D. tristachyum* but was clearly neither. Collections were made in August and November, 1993, from the same clone.

This plant has the general aspect of *D.* ×*sabinifolium* with a congested, tufted habit rather than a pseudo-monopodial habit such as characterizes *D. digitatum* and *D. tristrachyum* (Figure 1). This is due to the branching of upright stems near their bases and to the length of the lower branches which reach beyond the bases of upper branches. The plant is also similar to *D.* ×*sabinifolium* in its short, usually unbranched peduncle with one or two sporophylls on the peduncle below the strobilus. A hybrid origin, however, was suspected because the lateral branchlets are strongly dorsiventrally flattened, the lateral leaves are appressed rather than spreading, and the lower (ventral) leaves are reduced, all characteristics that do not occur in *D.* ×*sabinifolium*. Fur-

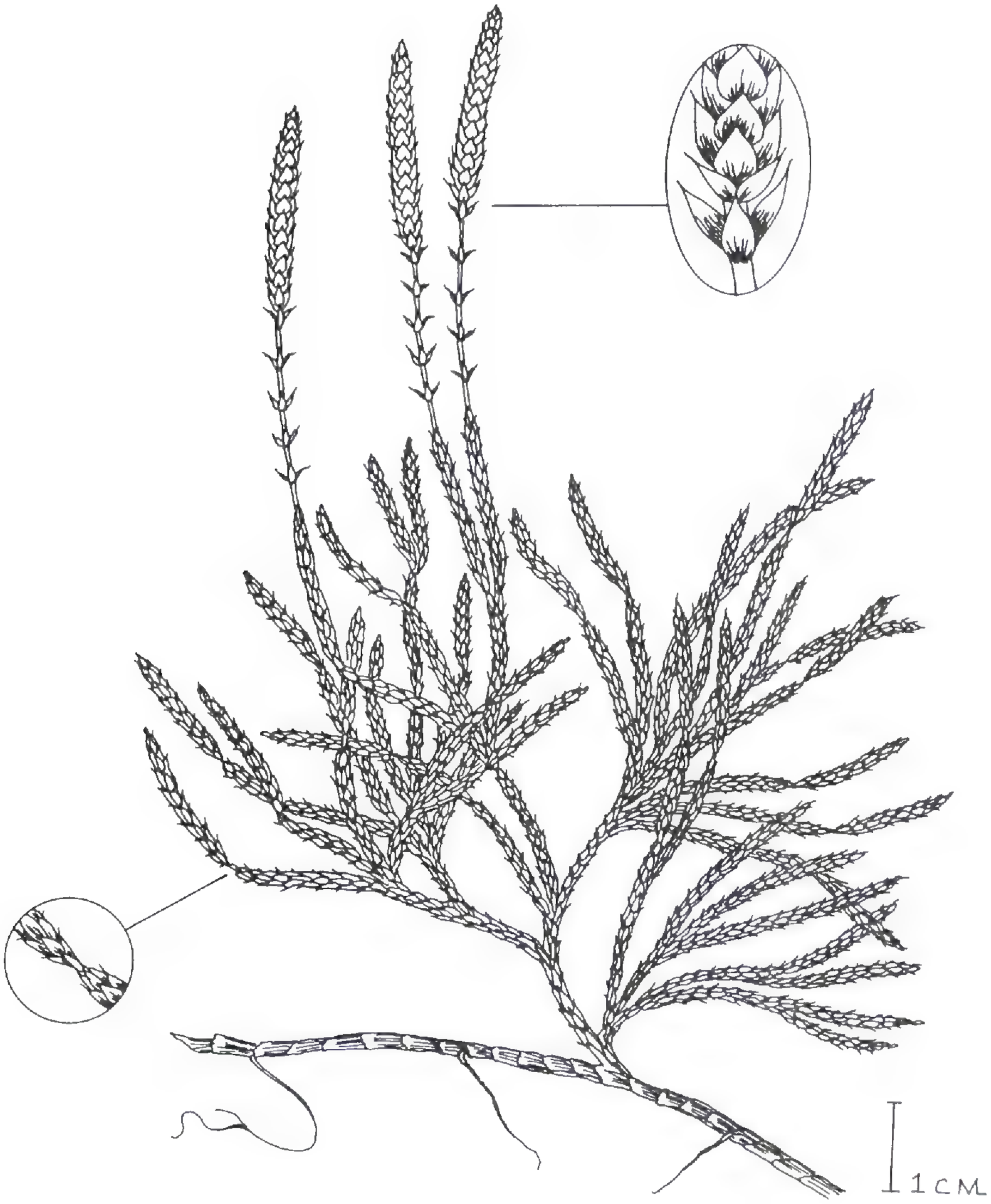

Figure 1. *Diphasiastrum digitatum* × *sabinifolium.* The influence of *D.* ×*sabinifolium* is indicated by the low branching, the indeterminate growth of branches as shown by annual constrictions, and the unbranched peduncle with sporophylls scattered at the base of the strobilus (see details). The broad, flattened branches, reduced lower leaves and broad sporophylls are evidence of *D. digitatum* parentage.

thermore, the plant overall is larger and stouter than typical *D.* ×*sabinifolium.*

A morphological analysis was undertaken to determine the identity of this puzzling plant. With such tests of hybridity as garden experiments, isozyme or DNA analysis lacking at present,

Table 2. Hybrid index comparing ten qualitative characters of the putative hybrid *D. digitatum* × *sabinifolium* and its parents. (2 = character as in *D.* ×*sabinifolium*; 1 = intermediate; 0 = character as in *D. digitatum*).

Character (from Wilce, 1965)	sab	dig × sab	dig
1. Habit congested due to branching low on upright stem, vs. pseudomonopodial	2	1	0
2. Branches indeterminate for 2 or more years, as shown by annual constrictions	2	2	0
3. Branches slightly glaucous, vs. bright green	2	1	0
4. Branches not or only slightly flattened dorsiventrally	2	0	0
5. Lower leaves not reduced, vs. reduced	2	1	0
6. Lateral leaves spreading vs. appressed	2	0	0
7. Lateral leaves with narrow base, vs. broad base	2	0	0
8. Fertile branch round with equal leaves (vs. flattened with reduced lower leaves)	2	2	0
9. Peduncle usually unbranched (vs. normally branched)	2	2	0
10. Sporophyll narrow (vs. broad)	2	0	0
Total	20	9	0

therefore, morphological comparisons give the strongest evidence of this plant's hybrid status.

A series of hybrid indices (modified from Wilce, *op. cit.*, pp. 112–114) were prepared to compare this plant with potential parents. From these, it was determined that *D. digitatum* and *D.* ×*sabinifolium* are the most likely parents. Table 2 is the index prepared on the basis of ten qualitative characters by which these probable parents differ. Of the ten, four character states (irregular, tufted habit; indeterminate branchlet growth; rounded fertile branch with isomorphic leaves; and unbranched peduncle) are closest to *D* ×*sabinifolium*. Six characters (green coloration; dorsiventrally flattened and appressed lateral leaves; broad bases of lateral leaves, reduced lower leaves, broad sporophylls) are closer to *D. digitatum*. The putative hybrid has an index score of 9, intermediate between the scores of *D. digitatum* (0) and *D.* ×*sabinifolium* (20).

Quantitative characters give a somewhat less clear picture (Table 3), since the hybrid is not medial in every character, but approaches one parent or the other, or exceeds the parents in

Table 3. Comparison of mean quantitative morphological characters, each based on 30 measurements of dried plants (*D. digitatum*, Gilman 93241, Wheelock, VT; *D. digitatum* × *sabinifolium*, Gilman 93246, Walden, VT and Gilman 92069, Marathon, Ont.). All measurements in mm. Standard deviations in parentheses.

Character	sab	dig × sab	dig
1. Branch width	1.42 (0.25)	2.01 (0.68)	2.52 (0.57)
2. Lower leaf width (base of free portion)	0.71 (0.09)	0.84 (0.12)	0.53 (0.12)
3. Lower leaf length (free portion)	2.28 (0.28)	1.32 (0.15)	1.05 (0.14)
4. Ratio of lower leaf width/length	0.311	0.636	0.505
5. Peduncle length	24.6 (7.2)	28.8 (6.24)	48.5 (7.6)
6. Strobilus length	21.6 (4.24)	30.6 (4.78)	22.0 (1.40)
7. Sporophyll width	2.28 (0.28)	2.02 (0.14)	1.88 (0.17)
8. Sporophyll length	2.08 (0.08)	1.98 (0.10)	1.84 (0.09)
9. Ratio of sporophyll width/length	1.09	1.02	1.02

a few cases. Branchlet width at 2.01 mm is intermediate between the parents. The free portions of the lower leaves are intermediate in length, but are somewhat wider than either parent. The peduncle length is intermediate, but closer to *D.* ×*sabinifolium*. Strobilus length is greater than either parent, indeed greater than average for any native species (Wilce, 1965); this may be an anomaly of the individual plant or may be the result of hybrid vigor. The sporophyll is intermediate in width and length, but approaches *D. digitatum* in ratio of width to length (the "complanatum type" of Wilce).

DISCUSSION

Accepting the hypothesis that *D.* ×*sabinifolium* is of hybrid origin, then this hybrid has three ancestral genomes, *D. digitatum*, *D. sitchense*, and *D. tristachyum*, presumably present in the proportion 2:1:1.

Deviations from some expected intermediate character states may be inherited from individually variable parents. *D.* ×*sabinifolium* is itself quite variable (Cody and Britton, 1989) and variations in certain characters may have been passed on to the hybrid. Alternatively, variations may be due to unequal contributions of the ancestral genomes, *D. digitatum, D. sitchense* and *D. tristachyum*. In particular, *D. sitchense* seems to be strongly

represented in the short unbranched peduncle (as opposed to the long and regularly forked peduncles of *D. digitatum* and *D. tristachyum*), and in the low-branched, tufted habit (as opposed to the pseudomonopodial habit of *D. digitatum* and *D. tristachyum*).

Another potential hybrid combination, between *D. sitchense* and *D.* ×*habereri* would have the same genomes in different proportion (1:2:1). On analogy with *D.* ×*sabinifolium*, such a hybrid should display *D. sitchense* characters even more strongly, i.e., it would be expected to have non-flattened branches, spreading lateral leaves, and unreduced lower leaves. Furthermore, this alternative is unlikely because neither parent is known in the immediate vicinity, whereas *D. digitatum* is abundant in the area and *D.* ×*sabinifolium* is known to occur nearby (D.S. Barrington, pers. comm.).

As noted above, species and hybrids in *Diphasiastrum* are morphologically distinct, and the hybrids are apparently fertile. The barriers that prevent the hybrids from back-crossing and rehybridizing to the point of swamping the parent species, which maintain their distinctions over broad ranges, have not been identified. The discovery of the hybrid discussed here is significant because it suggests at least the possibility of introgression and the formation of hybrid swarms. On the other hand, both its distinctiveness and its rarity confirm the current concepts of species within the group.

Although its spores are well-formed and may be viable, this hybrid is as yet known only from one site. There is no direct evidence that it is reproductively competent beyond surviving and slowly spreading as a single clone. For this reason I have chosen not to provide an epithet.

MATERIAL EXAMINED

Vermont: **Caledonia County**: Wheelock, highest pasture on E side of Ide Mountain, elevation ca. 540 m, *A. V. Gilman 93240*, 21 August and 27 November 1993 (VT, NEBC, MICH).

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P.O. BOX 82
MARSHFIELD, VERMONT 05658

THE NEW ENGLAND BOTANICAL CLUB
22 Divinity Avenue
Cambridge, MA 02138

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THE TAXONOMY OF *CAREX PETRICOSA* (CYPERACEAE) AND RELATED SPECIES IN NORTH AMERICA

PETER W. BALL AND MARGARET ZOLADZ

ABSTRACT

In North America the *Carex petricosa* group has generally been considered to consist of three species, *C. petricosa* and *C. franklinii* in western Canada and Alaska, and *C. misandroides* in eastern Canada. In addition a number of other species and varieties have been described in the past fifty years, but these have generally not been given formal recognition by subsequent authors. A morphological study of herbarium specimens of this group led to the conclusion that all of these taxa should be treated as a single species. The western and eastern populations differed in the proportion of flowers that were distigmatic. Western plants were mostly tristigmatic or had not more than 50% distigmatic flowers. Eastern plants were mostly distigmatic or had more than 50% distigmatic flowers. Consequently two varieties were recognised in *C. petricosa,* var. *petricosa* from the west, and var. *misandroides* (Fernald) Boivin from the east.

Key Words: *Carex* sect. *Aulocystis,* taxonomy, distribution, North America

INTRODUCTION

Carex petricosa Dewey is a member of the large section Aulocystis Dumortier. The section has been known under a variety of names, in particular section Ferrugineae (Mackenzie, 1935) and section Frigidae (Kükenthal, 1909). Kükenthal (1909) recognised over 50 species in the section, of which only 6 occurred in North America. In his monograph of North American *Carex* Mackenzie (1935) recognised 10 species in the section, of which 5 were endemic to the western mountains of the United States, just extending into southern British Columbia, 2 were widespread circumboreal arctic-alpine species, and 3 were subarctic-montane species endemic to Canada and Alaska. These latter 3 species, *C.*

petricosa, C. franklinii Boott and *C. misandroides* Fernald, form the group of species which is the subject of this paper.

The *Carex petricosa* group of species is difficult to define morphologically in an unambiguous way. The perigynia are more or less erect when mature, sparsely setose on the surface and tapering at the apex to an indistinct beak. The distribution of staminate and pistillate flowers in the inflorescence is extremely irregular, some individuals having a single terminal staminate spike and several lateral pistillate spikes, while others have an androgynous terminal spike (staminate at the apex, pistillate at the base), with some pistillate and some androgynous lateral spikes, often arranged in an irregular manner. The stigma number is also variable as all three species can have 2 or 3 stigmas, although 3 is predominant in *C. petricosa* and *C. franklinii* and 2 is predominant in *C. misandroides*. When Mackenzie prepared his monograph these species were known from very few collections. *Carex franklinii* and *C. petricosa* were known from a very few stations in the Rocky mountain range in Canada, while *C. misandroides* was known from a single station in Newfoundland and another in the Gaspé peninsular in eastern Quebec. Subsequent collections have extended the range of *C. franklinii* and *C. petricosa* to Alaska and the western Northwest Territories, and additional sites for *C. misandroides* have been found in Newfoundland and Quebec.

Since the publication of Mackenzie (1935) the North American species of the group have been the subject of two revisions. In both of these a number of new or additional taxa were recognised or described. Boivin (1948) described one new species, *C. distichiflora,* and two new varieties, *C. franklinii* var. *nicholsonis,* and *C. petricosa* var. *edwardsii.* Not to be outdone Raymond (1952) added two new species, *C. magnursina* and *C. lepageana,* and the first North American record of the Asian species *C. stenocarpa* Turcz. ex Besser. However, Raymond included *C. distichiflora* in the synonymy of *C. franklinii,* and treated *C. misandroides* as a variety of *C. franklinii.* Subsequent authors have tended to take a more conservative view of the group and have usually recognized two species in the west, *C. franklinii* and *C. petricosa,* with *C. misandroides* being included as a synonym or variety of *C. franklinii* (e.g., Hultén, 1968; Porsild and Cody, 1980; Packer, 1983). Boivin (1967) and Scoggan (1978) recognised only a single species with four varieties, and Welsh (1974) treated *C. franklinii* as a synonym of *C. petricosa.* The report of *C. stenocarpa* from

Alaska (Raymond, 1952) seems to have been overlooked as it is not mentioned in Hultén (1968) or Welsh (1974). In addition to North American names, Hultén included the Asian species *C. macrogyna* Turcz. ex Besser as a synonym of *C. franklinii.* Another, unpublished, name also appears on herbarium sheets. As noted by Raymond (1952), Fernald had named the earlier collections from Lac Mistassini, Quebec, as *C. mistassinica,* but this name was never validly published and Raymond treated the specimens so named as *C. franklinii* var. *misandroides.*

Initially the investigation was aimed at determining the status of *C. misandroides,* whether it could be retained as a taxon distinct from the western species, and also whether it was most similar to *C. franklinii* or *C. petricosa.* As the investigation progressed it became apparent that these questions could not be adequently addressed without a more thorough examination of the status of the western taxa of the group, including those published since Mackenzie (1935).

METHODS

The study was based entirely on herbarium specimens collected from North America and a small number from north east Asia. Approximately 250 specimens were examined from the following herbaria: ALA, CAN, DAO, MT, TRT, TRTE (acronyms according to Holmgren et al. 1990). The North American specimens represented a high proportion of the known stations of the taxa under investigation.

It proved difficult to classify specimens on the basis of morphology, so all plants from Newfoundland and Quebec were assigned to *C. misandroides,* except for the specimens named *C. mistassinica,* which were provisionally treated as a separate taxon. The post-1935 taxa are known only from specimens cited in the protologue and these were also treated as separate taxa, although in some cases the specimens were too immature to include in the morphologic analyses. *Carex petricosa* and *C. franklinii* proved difficult to distinguish based either on the names on specimens, or on the characters utilized in such works as Packer (1983). The specimens were eventually separated arbitrarily based on the width of the mature perigynium, specimens with the perigynium wider than 1.7 mm being allocated to *C. franklinii,* those with the perigynium narrower than 1.7 mm being allocated to *C. petricosa,*

and those with the perigynium 1.7 mm wide being allocated according to the name on the label.

Characters were selected based on those utilized by Mackenzie (1935), Boivin (1948) and Raymond (1952) to separate the taxa that they recognized. A few proved impossible to record satisfactorily, particularly the "curved" basal leaves emphasized by Raymond (1952) in his diagnosis of *C. magnursina,* and the color of the perigynia (dark brown versus yellowish brown) which to some extent depends on the age and state of development of the inflorescence. The number of stigmas was found to be quite variable on one individual. This was recorded by randomly choosing 5 perigynia in an inflorescence and reporting the number which had 2 stigmas. For specimens which had shed their stigmas the stigma number was based on the cross-sectional shape of the achene, biconvex for 2 stigmas and triangular for 3 stigmas. Because examination of the achenes is destructive only 3 perigynia were examined in these specimens. In a few specimens a large number of perigynia were available with visible stigmas and these were used to confirm that the method outlined above gave a reasonable estimate of the frequency of the two stigma numbers on one individual.

A total of 20 characters were recorded from the specimens examined, but not all could be utilised in the numerical analyses. Specimens were selected based on the presence of reasonably well-developed perigynia. Many specimens were collected too early in the season to have reached this stage of development, consequently it was sometimes necessary to use duplicate specimens to obtain a reasonably large sample for analysis. A total of 101 specimens were eventually included in the data set, 29 specimens of *C. petricosa* (including 2 determined as var. *edwardsii*), 27 specimens of *C. franklinii,* 24 specimens of *C. misandroides,* plus 2 specimens determined as *C. mistassinica,* 15 specimens of *C. macrogyna,* 2 specimens of *C. lepageana,* and 1 each of *C. distichiflora, C. magnursina* and *C. stenocarpa* (from Alaska).

Principal components analysis (PCA) and discriminant functions analysis (DFA) were performed using SYSTAT 5.0 (Wilkinson, 1990). PCA was used to obtain a broad overview of the variation in the data set and to determine whether there was any tendency to form groups. The data used in this analysis were standardised to zero mean and unit variance. All characters listed in Table 1 were included in the analysis except for STS which

Table 1. List of morphological characters recorded for the *Carex petricosa* group.

Character	Character Abbreviation
Stem height (cm)	STHT
Bract length (mm)	BRL
Bract sheath length (mm)	BRSL
Sex of the terminal spike	STS
Number of pistillate spikes	FSPN
Number of staminate spikes	MSPN
Number of hermaphrodite spikes	HSPN
Pistillate spike width (mm)	FSPW
Pistillate spike length (mm)	FSPL
Width of the staminate portion of the terminal spike (mm)	MSPW
Length of the staminate portion of the terminal spike (mm)	MSPL
Staminate scale length (mm)	STSCL
Staminate scale width (mm)	STSCW
Pistillate scale length (mm)	PSCL
Perigynium length (mm)	PERL
Perigynium width (mm)	PERW
Perigynium beak length (mm)	PERBL
Perigynium nerve number	PERNN
Stigma number	STN

was considered to be a variable that was not independent from MSPN.

DFA was used to obtain maximum separation of the four major taxa, *C. franklinii, C. macrogyna, C. misandroides* and *C. petricosa.* PERW was not included in this analysis as this character was used to define *C. franklinii* and *C. petricosa.* The other two taxa were defined using distribution as the main criterion. A classification procedure was used to assign the remaining taxa to one of the four groups.

RESULTS

Taxonomic Characters

It is not intended to review all the characters included in this study, but rather to consider those on which considerable emphasis has been placed in the past. Except as discussed below

none of the characters examined showed any significant difference between the four main taxa included in this study.

1. STEM HEIGHT. This character has been used to distinguish *C. franklinii* and *C. petricosa* (e.g., Porsild and Cody, 1980, Packer, 1983), and *C. franklinii* and *C. misandroides* (Raymond, 1952). Stem height was very variable and was poorly correlated with other diagnostic characters, particularly perigynium width (correlation coefficient 0.252).

2. TERMINAL SPIKE. Kükenthal (1909) placed *C. franklinii* and *C. petricosa* in different subsections of sect. Frigidae based on differences in the terminal spike. *Carex franklinii* was described as having an androgynous terminal spike, while *C. petricosa* was said to have a mainly staminate terminal spike. As pointed out by Raymond (1952) this character is very variable. Boott (1839) in his diagnosis of *C. franklinii* noted that the terminal spike could be both staminate and androgynous. Two collections from a population near Jasper, Alberta, close to the area from which the type of *C. franklinii* was collected, emphasize the point. Porsild 22537 (CAN) has an androgynous terminal spike (with perigynia 1.7 mm wide), and Porsild 22538 (CAN) has a staminate terminal spike (with perigynia 2.2 mm wide). In both *C. petricosa* and *C. misandroides* a staminate terminal spike is more frequent, but in both taxa androgynous spikes occur in about 50% of the specimens examined. This variation may occur in a single clone suggesting that this character is not under direct genetic control. There is a tendency for robust plants to have an androgynous terminal spike and for small plants to have a staminate terminal spike, but this is not at all consistent (the two Porsild collections cited above have stem heights of 48 cm and 51 cm respectively).

3. LATERAL PISTILLATE SPIKE SIZE. Raymond (1952) emphasized this character when describing *C. lepageana* and *C. magnursina,* stating that these two species had pistillate spikes 8–25 × 3–4 mm, while *C. petricosa, C. franklinii* and *C. misandroides* had pistillate spikes 8–15 × 6–9 mm. *Carex petricosa* was found to have a spike length of 7–29 mm (mean 15 mm), while *C. misandroides* and *C. petricosa* had a similar mean but narrower range. Spike width showed a similar pattern, with *C. petricosa* having spikes 3–7 mm wide. All three taxa had a mean width close to 5 mm.

4. PERIGYNIUM SIZE. Perigynium width is the character most frequently used to separate *C. petricosa* and *C. franklinii.* Ray-

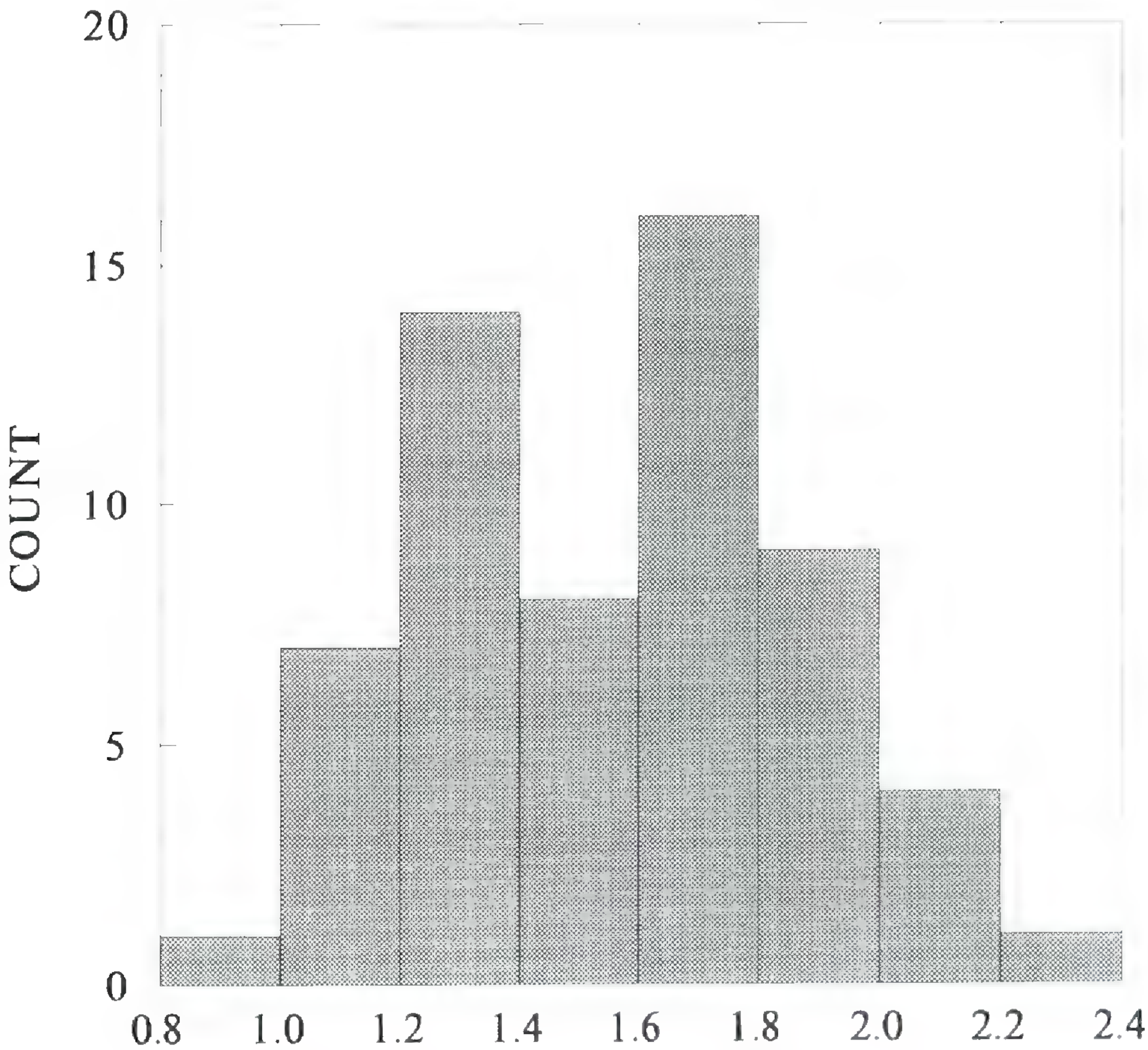

Figure 1. Histogram of perigynium width (mm) of western North American specimens of the *Carex petricosa* group.

mond (1952) gave the perigynium width of *C. petricosa* as 1.5–1.75 mm and that of *C. franklinii* and *C. misandroides* as 2–2.5 mm. Other authors, such as Mackenzie (1935), gave a similar difference. Porsild and Cody (1980) claim a difference in perigynium length giving 5–6 mm for *C. franklinii* and 4–5 mm for *C. petricosa*. In this investigation perigynium length showed no clear difference between the three main North American taxa. *Carex petricosa* was the most variable with a range of 3.5–5.5 mm, while *C. franklinii* had a range of 3.8–5.3 mm and *C. misandroides* 3.9–5.2 mm. Perigynium width was eventually used to arbitrarily separate *C. franklinii* from *C. petricosa*. The clear disjunction in perigynium width claimed by Raymond (1952) and others does not exist. A histogram of perigynium width (Figure 1) for the

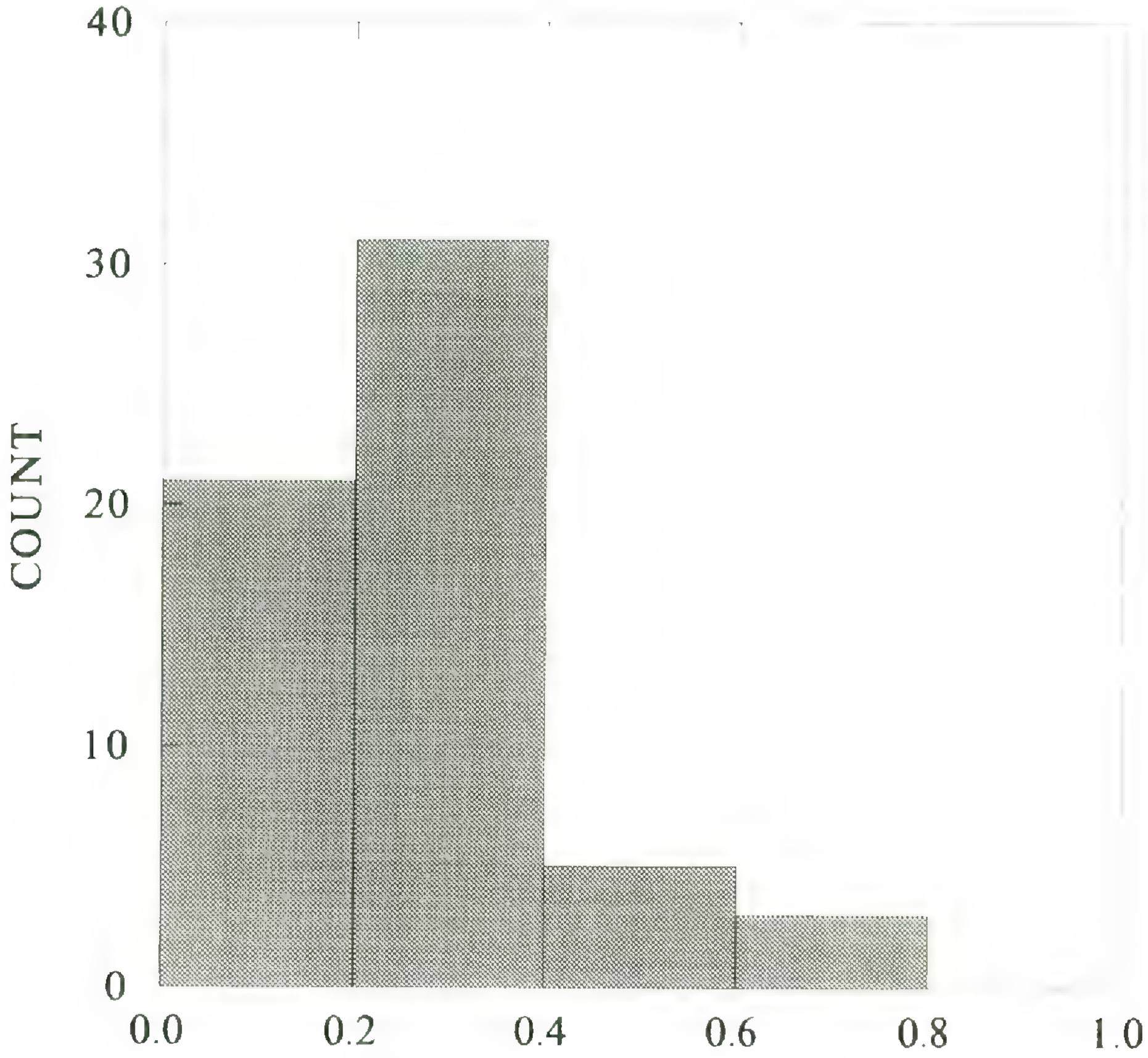

Figure 2. Histograms of the proportion of flowers, on each specimen, with two stigmas. **A.** Western North America.

western North American taxa shows a somewhat bimodal distribution with peaks at about 1.3 mm and 1.7 mm but there is no discontinuity. *Carex misandroides* has a perigynium width matching that of *C. petricosa* rather than that of *C. franklinii.*

5. STIGMA NUMBER. This character was emphasized by Fernald (1915) and Mackenzie (1935) in their descriptions of *C. misandroides.* Both acknowledged that there was some variation in the stigma number, but no data were presented to indicate the extent of the variation. In this study it was found that the eastern populations have a preponderance of flowers with two stigmas, while the western populations have a preponderance of flowers with three stigmas (Figure 2). Approximately 10% of the western specimens examined either had a preponderance of flowers with

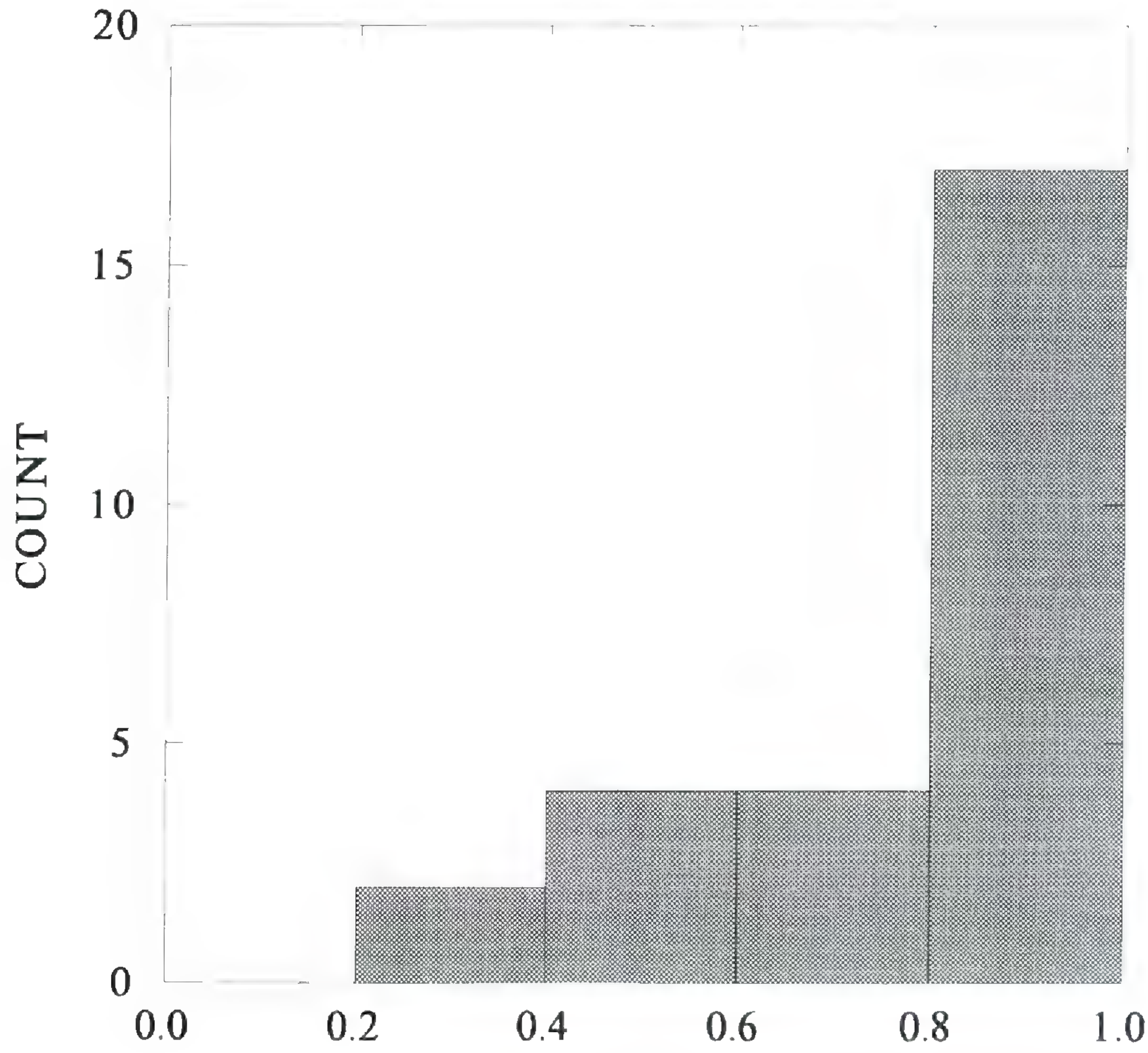

Figure 2. Continued. **B.** Eastern North America.

two stigmas or had flowers with two and three stigmas about equal in frequency. In the east about 20% of plants had a preponderance of flowers with three stigmas or had flowers with two and three stigmas about equal in number. No western specimens were entirely distigmatic and no eastern specimens were entirely tristigmatic. The Asian species, *C. macrogyna,* was similar to the western North American taxa in this character.

Multivariate Analyses

PCA showed a more or less normal distribution of specimens in the space defined by the first three components, with no tendency to form clusters (Figure 3). The first component accounted for 23.7% of the variance in the data set, with a large number of

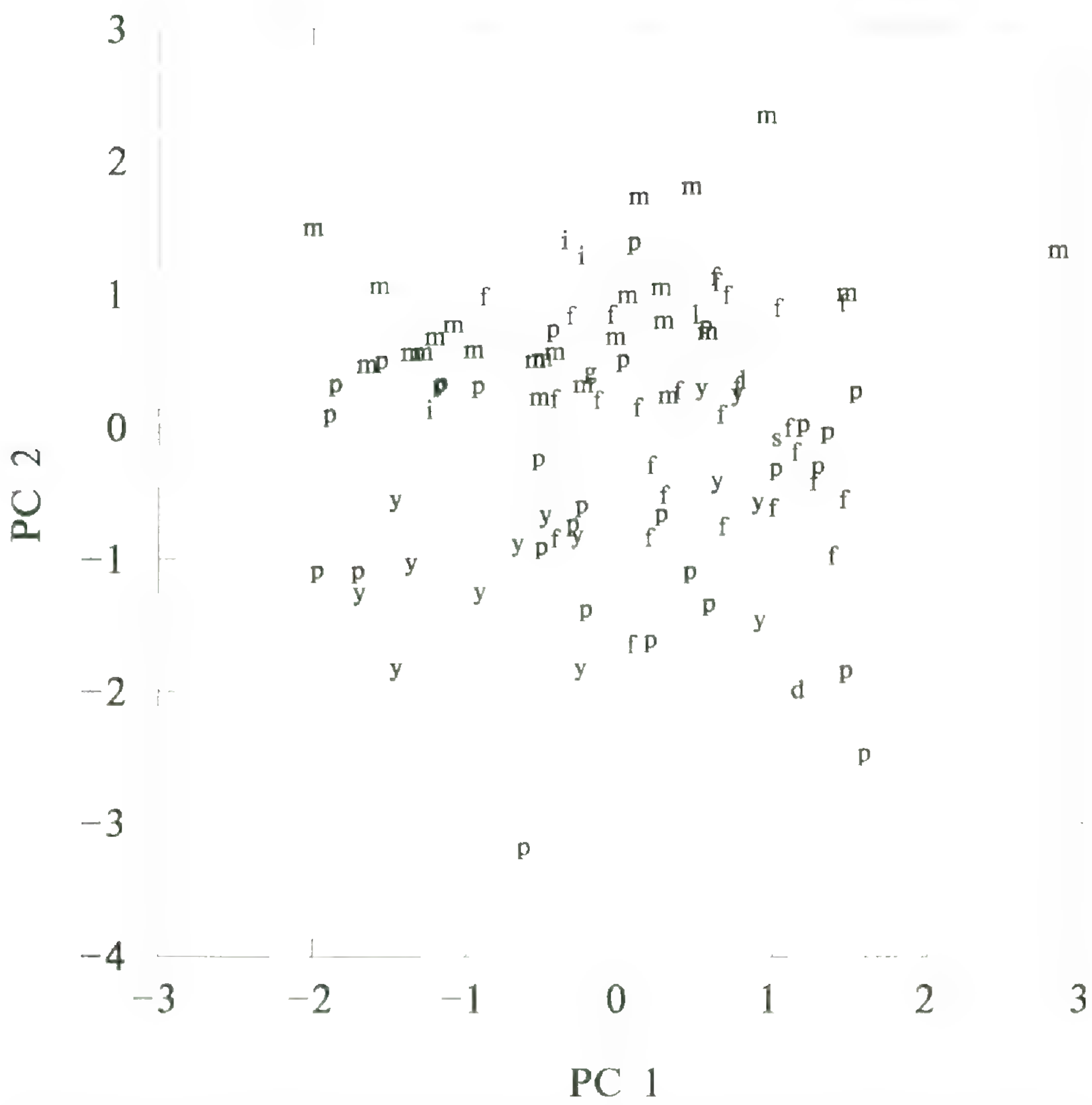

Figure 3. Bivariate plot of OTU's of the *Carex petricosa* group on principal components 1 and 2. Letters identify taxa according to Table 2.

size variables having high loadings. Most specimens of *C. franklinii* had a positive score on this axis, while *C. macrogyna, C. misandroides* and *C. petricosa* had individuals with both high positive and high negative scores. The second component accounted for 10.6% of the variance in the data set, with staminate spike number, stigma number, perigynium beak length and pistillate spike number having high loadings. *Carex misandroides* (together with *C. mistassinica*) had positive scores on this axis, but they were mixed with individuals from the other main taxa. The third component showed no useful groupings. The specimen determined as *C. stenocarpa* was placed well within the main cluster, and was neither marginal nor disjunct from the other taxa.

DFA gave only a slightly better grouping of specimens than the PCA (Figure 4). *Carex misandroides* formed a reasonably discrete group on the first DF, with only 4 of 24 specimens being misclassified (Table 2). The two specimens labelled as *C. mistassinica* were classified in this group, as might be expected. Stigma number was the most important discriminating variable, with bract sheath length as a secondary character. The second DF weakly separated *C. franklinii, C. macrogyna* and *C. petricosa.* With *C. petricosa* only 16 of 29 specimens were correctly classified, the remaining 13 specimens being evenly distributed among the other three taxa. *Carex franklinii* had 19 of 27 specimens correctly classified, and *C. macrogyna* had 10 of 15 correctly classified. The type of *C. magnursina* was classified with *C. misandroides,* but was close to the boundary with *C. petricosa.* A specimen from Nome, Alaska, determined by Raymond as *C. stenocarpa* was classified as *C. franklinii,* although it was close to the boundary with *C. petricosa.* The specimens of *C. lepageana* were also classified as *C. franklinii.*

DISCUSSION

The complete failure of the multivariate analyses to satisfactorily differentiate the taxa included in this study is strong evidence to support the view that there is only one species in this group. The exclusion of perigynium width from the DFA might account for some of the problems with group separation in that analysis, but it is clear from Figure 1 that there is no clear disjunction in this character as suggested by previous authors. *Carex lepageana, C. magnursina* and *C. distichiflora* fall well within the range of variation exhibited by the group as a whole. Likewise the specimen determined as *C. stenocarpa* appears to be a part of this group. Although no reliably determined Asian specimens of *C. stenocarpa* were examined, this species is described as having the larger leaves 4–6 mm wide (Kreczetowicz, 1935), while the Alaskan specimens have leaves not exceeding 3 mm wide, the same range as the *C. petricosa* group. The status of *C. macrogyna* is still unclear. The analyses support Hultén's (1968) view that *C. macrogyna* should be treated as a synonym of *C. petricosa,* especially given the broader circumscription of *C. petricosa* proposed above. However, most of the specimens included in the analyses came from the subarctic regions of Russia, while *C. macrogyna* was described from the mountainous area bordering

Table 2. Classification of specimens in the *Carex petricosa* group based on DFA. Rows are the groups to which specimens were assigned; columns are the classification according to the DFA.

	P	M	F	Y	Total
C. petricosa P	14	3	7	5	29
C. misandroides M	1	20	2	1	24
C. franklinii F	1	1	19	5	26
C. macrogyna Y	2	1	0	11	14
C. lepageana L	0	0	2	0	2
C. mistassinica I	0	3	0	0	3
C. magnursina G	0	1	0	0	1
C. stenocarpa S	1	0	0	0	1
C. distichiflora D	1	0	0	0	1
Total	20	29	30	22	101

Mongolia. Without a more extensive study of the group in Asia it seems prudent to not include *C. macrogyna* as a synonym of *C. petricosa* at this time. It does seem clear that the Asian subarctic populations are not distinct from *C. petricosa,* and these should be included in that species.

The final question concerns the status of *C. misandroides.* This taxon is disjunct from all the others by several thousand kilometers. Between 80% and 90% of specimens can be correctly classified using stigma number alone, without knowledge of the origin of the specimen. No other characters can be used to distinguish *C. misandroides* from the western taxa. Bract sheath length, which had a high value on the first DF together with stigma number, is much too variable. *Carex misandroides* has the highest mean value for this character, but the range, 3–38 mm, completely includes all the western taxa. Stem height shows some slight difference, with *C. misandroides* tending to be shorter than other taxa. Most plants of *C. misandroides* have stems in the range 20–35 cm high, with the extremes in the range 10–55 cm. In the western taxa the normal stem height is in the range 20–50 cm,

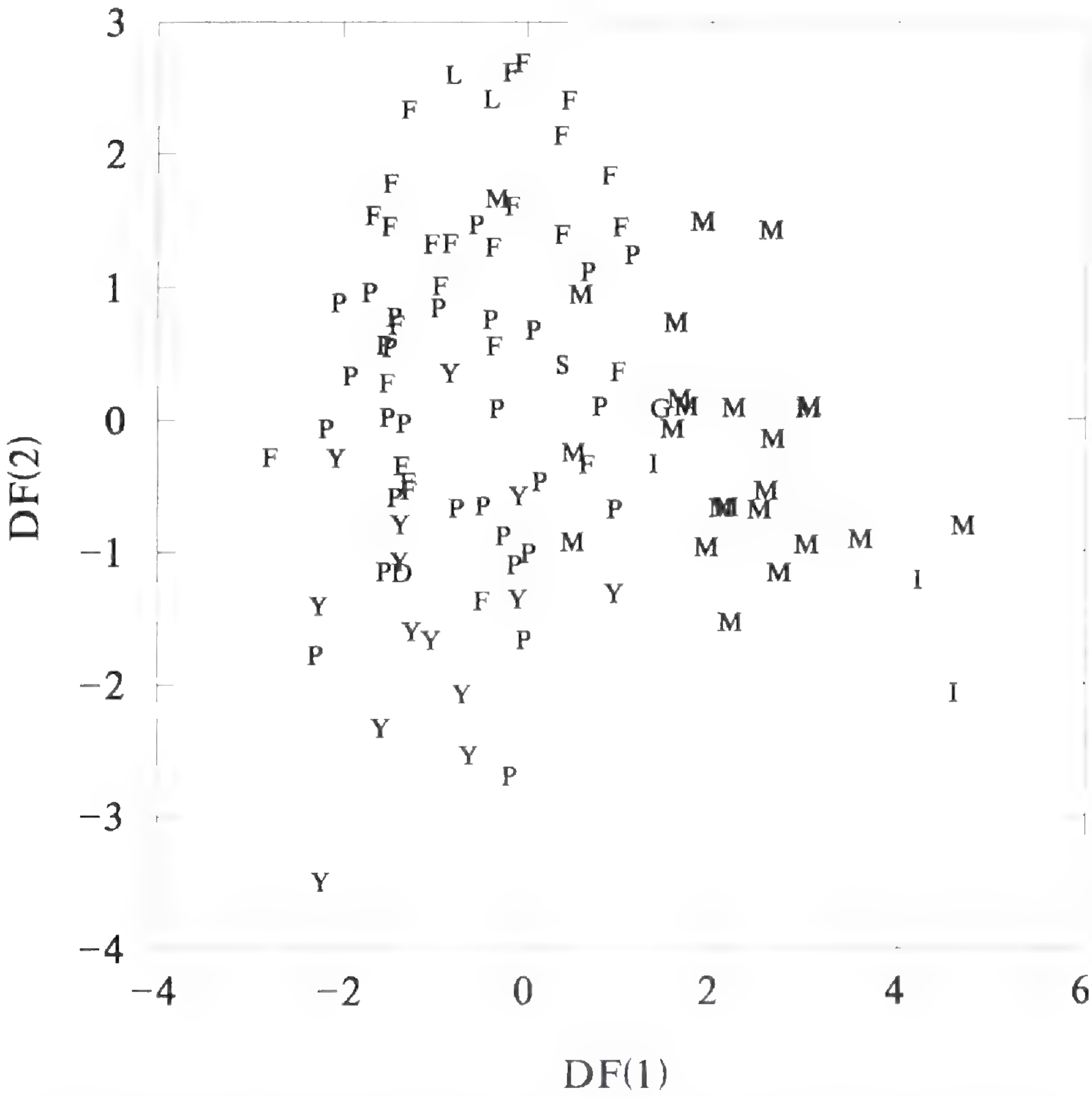

Figure 4. Bivariate plot of OTU's of the *Carex petricosa* group on discriminate functions 1 and 2. Letters identify taxa according to Table 2.

with an extreme range of 10–80 cm. The lack of any consistent morphological difference between *C. misandroides* and the other taxa in the group precludes the recognition of this as a distinct species. On the other hand the geographical isolation combined with a morphological feature which reliably classifies over 80% of individuals suggests that recognition at infraspecific rank is justified. The distribution of *Carex petricosa* in North America is given in Figure 5.

TAXONOMIC SUMMARY

1. **Carex petricosa** Dewey, Amer. J. Arts Sci 29: 246. 1836. Summits of Rocky mountains (probably west of Jasper, Alberta).

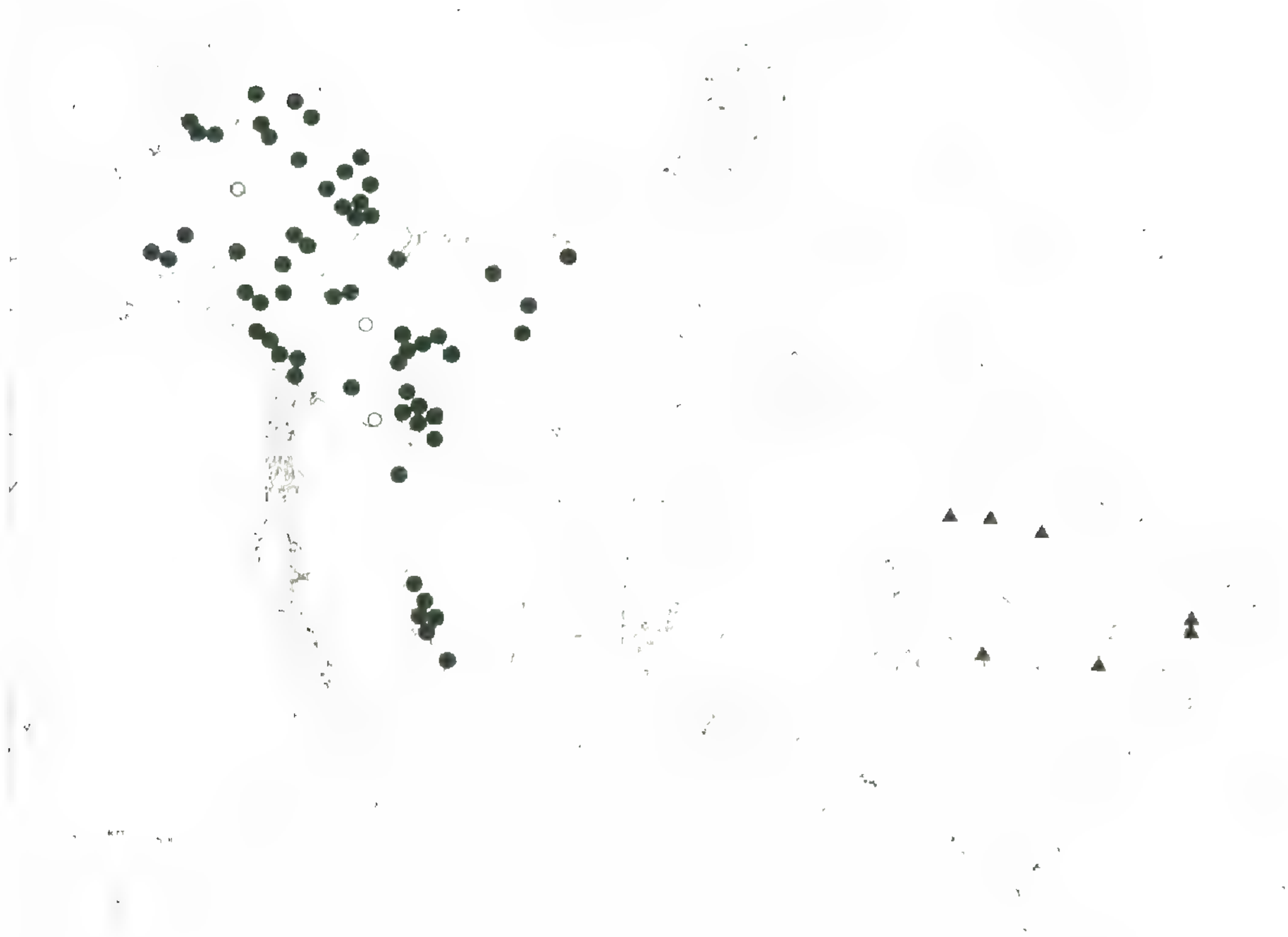

Figure 5. Distribution of *Carex petricosa* in North America. Circles = var. *petricosa*; triangles = var. *misandroides*. Solid symbols indicate specimens examined in this study; open symbols indicate literature records.

Drummond 283 (HOLOTYPE: Herb. Dewey, GH, photo CAN!, MT!, ISOTYPE: K, photo CAN!).

a. variety **petricosa**

Carex franklinii Boott in Hooker, Fl. bor.-am. 2: 217. 1839. Rocky mountains (near Jasper, Alberta). *Drummond 293* (HOLOTYPE: K, photo CAN!, MT!).

Carex distichflora Boivin, Naturaliste Canad. 75: 206. 1948. NORTHWEST TERRITORIES: Canol road, Mackenzie range, Sekwi river, mile 174E, pump station 5, 6 Sept. 1944. *Porsild and Breitung 11848* (HOLOTYPE: DAO!).

Carex mangursina Raymond, Canad. Field-Naturalist 66: 100. 1952. NORTHWEST TERRITORIES: Great Bear Lake, Harrison river, McTavish arm. 30 July 1948. *Steere et al. 3228* (HOLOTYPE: MT!).

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DEPARTMENT OF BOTANY
ERINDALE CAMPUS, UNIVERSITY OF TORONTO
MISSISSAUGA, ONTARIO, L5L 1C6, CANADA

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POLLEN AND PUBESCENCE CHARACTERISTICS OF *OXALIS GRANDIS* SMALL

DARRELL MOORE, DALLAS MULLINS AND FOSTER LEVY

ABSTRACT

Pubescence in *Oxalis grandis* Small was analyzed as a constellation of characters describing the numbers, types, orientations, and lengths of hairs on different regions of the plants. Pubescence is a complex character whose components vary independently with no obvious geographical or ecological correlates. Hirsute plants occur sporadically throughout the range of the species, but extreme expression of the entire suite of pubescence characters is restricted to one population. A correlation analysis indicates that pubescence in *Oxalis grandis* is most likely under complex genetic control and is therefore valuable as a taxonomic character. An analysis of pollen size utilizing plants from two populations representing extremes in pubescence shows significant differences between flower morphs. For corresponding morphs, pollen from the population with pubescent plants is larger. These studies have demonstrated high levels of intraspecific polymorphism within *Oxalis grandis*.

Key Words: character analysis, heterostyly, *Oxalis,* pollen, pubescence

INTRODUCTION

The genus *Oxalis* comprises species with heterostylous and homostylous flowers. *Oxalis grandis* Small, a resident of the southern Appalachian Mountains and Ohio River Valley, is tristylous with marked size differences among the style lengths of its three flower morphs (Eiten, 1963). Each style morph has two whorls of functional stamens. Members of the species possess characteristics of subsection Strictae, section Corniculatae: a creeping rootstock, spreading pedicels and septate trichomes. *Oxalis grandis* is further distinguished by relatively large leaflets bordered by a purple margin (Wiegand, 1925). All individuals from a population inhabiting lower and middle slopes of bluffs along the Watauga River in Sullivan and Washington Counties of northeastern Tennessee are extremely hirsute on all parts of the plant and thus are distinguished easily from those of more typical populations (Levy and Moore, 1993). These morphological differences persist when plants are transplanted to a common greenhouse environment and in a growth chamber when new ramets are propagated from root cuttings (F. Levy and D. Moore, unpublished data).

The extreme intraspecific variation encompassed by the Wa-

tauga River population in comparison to more typical populations provided an opportunity for an in-depth examination of the pubescence phenotype. Our objective was to provide a full description of the morphological differences related to pubescence and to conduct a herbarium search for *Oxalis grandis* specimens with extreme amounts of pubescence. We then performed a character correlation analysis to assess whether pubescence is under simple or complex genetic control. Specific goals of the study were to determine whether (i) the extremely pubescent phenotype is unique to the Watauga River population, (ii) there are geographic or ecological correlates associated with pubescence, (iii) expression of components of pubescence vary independently. Consequently, we have dissected pubescence into several qualitative and quantitative components and examined the expression of each in individual plants.

In the most recent treatment of subsection Corniculatae, Eiten (1963) considered qualitative components of epidermal vestiture. Eiten's implicit assumption was that each component represented an independent character. If pubescence is a simple character with a simple genetic basis, or if it is environmentally determined, then it has minimal taxonomic value (Rollins, 1958). On the other hand, if pubescence represents the expression of several independent characters then it merits more attention in assessing degrees of differentiation. In this study, we use correlation analysis to assess the complexity of the pubescence phenotype and as a test of Eiten's assumption of independence.

A second objective of the study is an analysis of pollen sizes of the three flower morphs of *O. grandis* to determine whether pollen diameter differs among flower morphs and whether pollen size differs between populations. For this analysis we compared pollen from two populations, the Watauga River population and a population in a more typical habitat for the species (mesic forest at Iron Mountain Gap, Unicoi County, TN).

SECTION I—PUBESCENCE

METHODS

Pubescence was measured on ten plants from each of two study populations. Of these ten plants, four and three were fresh and the remainder recently collected and dried, from the Iron Moun-

tain Gap and Watauga River populations, respectively. Plants were carefully chosen to encompass the range of mature plant size, habitat and geographical location within each population. Only mature, flowering or fruiting specimens were included. The numbers of nonseptate hairs (no septate hairs occur on leaflets) were counted within 5 × 5 mm squares on the abaxial and adaxial leaflet surfaces. These grids were displaced a minimum of 2 mm from the midvein of one leaflet on each plant. For a subset of plants, hairs were counted on three different leaves, but preliminary analysis showed little variation and so, for the remainder, only one grid was counted per plant. Nonseptate and septate hairs also were counted on the circumference of one centimeter lengths of (i) the middle of a petiole, (ii) a section of the stem from the upper one-third of the plant (upper stem), and (iii) a section of the stem from the lower third of the plant (lower stem). Also measured were the maximal lengths of leaflet hairs (all nonseptate) and the septate and nonseptate hairs on stems. All counts and measurements were conducted at 40× under a dissecting microscope.

The analysis identified a suite of eleven pubescence characters by which the two populations may be differentiated (Table 3). We measured the same set of characters in a survey of herbarium specimens to determine (i) whether the extremely pubescent phenotype of the Watauga River population was unique or if a continuum of variation existed within the species, and (ii) whether individual characters related to pubescence vary independently. For the detailed analysis, we chose only herbarium specimens possessing some hairs on their leaves, that is, specimens showing at least a slight tendency toward a hirsute phenotype. The screen for pubescent phenotypes included specimens from the following five herbaria: UNC (51 sheets), TENN (31 sheets), VPI (25 sheets), WVA (57 sheets), and the collection at EAST TENNESSEE STATE UNIVERSITY (10 sheets).

DATA ANALYSIS. For each of the five regions for which hairs were counted (abaxial and adaxial leaf blades, petioles, upper and lower stems), separate Kruskal-Wallis tests were conducted to compare the number of hairs between populations. This nonparametric test was chosen because of heteroscedasticity of variances among populations. Separate analyses were carried out for septate and nonseptate hairs. G tests were used to compare proportions of septate and nonseptate hairs. These tests were con-

ducted first within populations to determine whether proportions varied in different regions of plants and then corresponding regions of plants were compared among populations.

Associations between pairs of pubescence characters were estimated by Pearson Correlation Coefficients (CORR procedure, SAS Institute, 1982). These correlations were computed between all possible pairs of characters within: (i) the sample of 10 plants from the Iron Mountain Gap population, (ii) the sample of 10 plants from the Watauga River population and, (iii) the sample of 14 herbarium specimens exhibiting hairs on the leaves. Eight characters were included for the Iron Mountain Gap and Watauga River samples (there was no variation for any of the three hair-length characters within either population), and eleven characters in the herbarium sample (Table 3).

RESULTS

The Iron Mountain Gap population exhibited the complete absence of hairs on the abaxial and adaxial leaf surfaces, except for sparse nonseptate hairs along the midvein and leaflet margins. This contrasted strongly with the abundant nonseptate hairs on both leaf surfaces of all plants from the Watauga River population (Table 1). Although the midvein of leaflets from both populations had nonseptate hairs, those of the Watauga River population were longer (1.0–1.5 vs 0.7 mm) and were patent in contrast to the appressed hairs of the Iron Mountain Gap population. Both septate and nonseptate hairs occurred throughout the vegetative axis (stems and petioles) of plants from both populations, but the mean number of hairs was significantly greater in the Watauga River population for each hair type in each region of the plant (Table 1). Furthermore, the ranges of variation in the number of nonseptate hairs on petioles, as well as on upper and lower stems, did not overlap between the two populations (Table 1).

The ratio of septate : nonseptate hairs increased significantly on the lower stems within both populations, but did not differ between upper stems and petioles (Table 2). Comparisons between populations showed that the relative contribution of septate hairs on petioles was similar, but for upper and lower stems, it was significantly higher in the Iron Mountain Gap population (Table 2).

The unusual Watauga River population can be characterized

Table 1. Pubescence characteristics of two populations of *Oxalis grandis*. Entries represent the mean, standard deviation (SD) and range for numbers of septate and non-septate hairs in different regions of plants. The Kruskal-Wallis statistics and their associated probabilities (* <0.05, *** <0.001) are given for comparisons among populations.

	Stem							
	Upper		Lower		Petiole		Leaflet	
	Non-septate	Septate	Non-septate	Septate	Non-septate	Septate	Abaxial	Adaxial
Iron Mountain Gap								
Mean (SD)	53.3 (17.6)	25.4 (9.9)	22.2 (18.6)	69.1 (32.8)	45.7 (14.0)	15.0 (7.3)	0	0
Range	29–89	9–44	8–57	39–149	30–78	8–30	0	0
Watauga River								
Mean (SD)	375.0 (143.7)	67.8 (65.0)	250.2 (191.8)	203.3 (122.7)	209.1 (87.0)	39.9 (24.4)	79.9 (26.5)	131.3 (60.9)
Range	190–585	4–235	123–780	46–470	115–410	11–73	30–119	49–225
Kruskal-Wallis	14.3***	5.0*	14.3***	8.3***	14.3***	6.2*		

by a suite of traits that includes; abundant, long, patent, nonseptate hairs on the abaxial and adaxial leaf surfaces; and abundant, long, patent septate and nonseptate hairs on the stems. Thus, these plants have an easily observed dense covering of relatively long hairs throughout the plant; a hand lens is not necessary to distinguish this phenotype.

CHARACTER CORRELATIONS. In the Iron Mountain Gap population, four of the 28 possible correlations between pairs of characters were significant (Table 3). Several significant character correlations (seven of the possible 28) occurred in the Watauga River population (Table 3), and five of these were highly significant. The correlation matrix for the sample of herbarium specimens consisted of eleven characters (three hair-length characters were included in addition to the eight hair type characters). Six of the 55 possible correlations were significant (Table 3). All six significant correlations were positive and concerned characters related to numbers of nonseptate hairs. Six of the ten possible nonseptate/nonseptate correlations were significant. There were no significant correlations involving septate/nonseptate pairs of characters or any combination of hair length characters. In summary, there were significant correlations involving septate and nonseptate hairs within and between organs in the Watauga River sample, but in the herbarium sample, the only significant associations involved nonseptate hairs.

SECTION II—POLLEN

METHODS

Oxalis grandis is morphologically tristylous, that is, "the stigmas occur at a level different from the level of either of the two rings of anthers: either below both (short-styled), between them (midstyled), or above both (long-styled)" (Eiten, 1963). For most flowers, pollen was sampled from both anther whorls of each flower. Slides of pollen samples were prepared from fresh material in the field. A freshly dehisced anther was touched to a glass slide that was then stained with lactophenol aniline-blue dye. Because *Oxalis grandis* propagates clonally from rhizomes, sampled plants were separated by a minimum of 3 m. The samples from each population spanned the physical extent of each population and encompassed an area of approximately 5 km^2 and 20 km^2 in the

Table 2. Relative contribution of septate hairs (expressed as percent septate) to pubescence on different parts of *Oxalis grandis* in two populations. The value of the *G* statistic is given for each population comparison, asterisks refer to probabilities associated with each value of *G*. M = Iron Mountain Gap, W = Watauga River, ns = non-significant, ** <0.01, *** >0.001.

	Population		*G* (between populations)
	M	W	
Petiole	24.7%	16.0%	2.4 ns
Upper stem	32.3%	15.3%	10.4**
Lower stem	75.7%	44.8%	30.2***
Upper vs. lower stem (within populations)			
G	33.4***	95.8***	

Iron Mountain Gap and Watauga River populations, respectively. The diameters of ten pollen grains were measured from each anther using an ocular micrometer at 400×.

DATA ANALYSIS. For each style morph in each population, a separate one-way analysis of variance (ANOVA) was used to compare pollen diameters between the two anther whorls of a morph. None of these comparisons showed significant differences and therefore, anther samples from the two whorls of a flower morph were pooled for comparisons among style morphs within and between populations. Pollen diameters among style morphs within populations were compared by one-way ANOVA followed by Student-Newman-Keuls (SNK) comparisons among means (SAS Institute, 1982). To compare pollen diameters between populations, each morph was treated separately in a one-way ANOVA followed by SNK comparisons among means.

RESULTS

Differences in pollen diameter between anther whorls were not significant for any of the three flower morphs within either population, although sample sizes for some comparisons were low (Table 5). Nevertheless, there were significant differences in pollen diameter among flower morphs within each population. In both populations, pollen from the short-styled morph was significantly larger than pollen from the two other morphs (Table 6). For all three flower morphs, pollen from plants in the Watauga River population was larger than pollen from the corresponding morph

Table 3. Character correlations within (A) the Iron Mountain Gap population, (B) the Watauga River population, and (C) a sample of selected herbarium specimens of *Oxalis grandis*. For each significant correlation, the Pearson Correlation Coefficient and its associated probability is shown. Character correlations that were significant in two of the sample groups are denoted by a common symbol.

Correlated Characters	Coefficient	*P*	Shared Correlations
A. Iron Mountain Gap			
StUpNS:StUpS	0.68	0.03	*
StUpNS:StLoNS	0.73	0.02	#
StLoNS:StUpS	0.70	0.02	
StLoS:PetS	0.68	0.03	+
B. Watauga River			
AbLf:AdLf	0.81	0.004	○
AbLf:StLoNS	0.65	0.04	
StLoNS:PetNS	0.84	0.002	
StLoNS:StLoS	0.82	0.004	
StLoS:PetS	0.80	0.006	+
StLoNS:StLoS	0.82	0.004	
StUpNS:StUpS	0.63	0.05	*
C. Selected Herbarium Sample			
AbLf:AdLf	0.55	0.04	○
AdLf:PetNS	0.54	0.05	
AdLf:StUpNS	0.84	0.0001	
AdLf:StLoNS	0.82	0.0003	
PetNS:StUpNS	0.72	0.004	
StUpNS:StLoNS	0.58	0.03	#

Key to Acronyms: number of hairs, adaxial leaflet surface, AdLf; number of hairs, abaxial leaflet surface, AbLf; number of nonseptate hairs, petiole, PetNS; number of septate hairs, petiole, PetS; number of nonseptate hairs, upper stem, StUpNS; number of septate hairs, upper stem, StUpS; number of nonseptate hairs, lower stem, StLoNS; number of septate hairs, lower stem, StLoS; nonseptate hair length, abaxial leaflet surface, LfHr; nonseptate hair length, stem and petiole, StHrNS; septate hair length, stem and petiole, StHrS.

in the Iron Mountain population (Table 6) and these differences were highly significant for the mid- and long-style morphs (ANOVA results: short-styled, $F = 2.96$; df = 1, 12; $P = 0.11$; mid-styled, $F = 26.6$; df = 1, 15; $P = 0.0001$; long-styled, $F = 8.5$; df = 1, 31; $P = 0.006$).

DISCUSSION

PUBESCENCE. In a study of *Oxalis* section Corniculatae, Wiegand (1925) noted extreme intraspecific variation in pubes-

Table 4. Characteristics of herbarium specimens[a] of *Oxalis grandis* that showed some leaf hairs. An "X" indicates expression of the character was within the range of variation observed within the Watauga River population. "Total W" indicates the number of Watauga River-like characters of the eight characters analyzed on each plant. " # Plants" refers to the number of test plants (max. = 14) that show the Watauga River-like phenotype for each character. C1 and C2 serve as controls since they were Watauga River site specimens collected prior to the current study. Acronyms as in Table 3.

	Character								Total
Plant	AbLf	AdLf	PetNS	StUpNS	StLoNS	LfHr	StHrNS	StHrS	W
1.	X								1
2.				X					1
3.					X				1
4.								X	1
5.	X		X						2
6.	X		X						2
7.	X					X			2
8.	X		X		X			X	4
9.	X	X	X	X	X				5
10.	X	X		X	X	X			5
11.	X	X	X	X				X	5
12.	X	X		X	X	X		X	6
13.	X	X	X	X	X	X			6
14.	X	X	X	X	X	X			6
C1.	X	X	X	X	X	X	X	X	8
C2.	X	X	X	X	X	X	X	X	8
# Plants	11	6	7	7	7	5	0	4	

[a] Key to herbarium specimens: 1. VIRGINIA, **Scott Co.**, summer 1958, *E. Elliott s.n.* (EAST TENNESSEE STATE UNIVERSITY); 2. VIRGINIA, **Wythe Co.**, open woods, 28 June 1910, *FSH s.n.* (VPI); 3. KENTUCKY, **Rockcastle Co.**, road bank along Rockcastle River, 17 June 1961, *H. E. Ahles 54501 with H. Smith* (UNC); 4. KENTUCKY, **Pulaski Co.**, mixed hemlock-hardwoods, Daniel Boone National Forest, 23 July 1970, *E. M. Browne and E. T. Browne Jr. 70K15.19* (UNC); 5. TENNESSEE, **Unicoi Co.**, Unaka Island, 8 June 1974, *C. L. Shepard 168* (EAST TENNESSEE STATE UNIVERSITY); 6. WEST VIRGINIA, **Hancock Co.**, Newmans Bridge, 21 June 1963, *J. Bonar s.n.* (WVA); 7. KENTUCKY, **Menifee Co.**, Red River Gorge, rich moist woods, 28 May 1969, *P. D. Higgins 1401* (UNC); 8. WEST VIRGINIA **Raleigh Co.**, 25 May 1940, *J. P. Tosh s.n.* (WVA); 9. TENNESSEE, **Pickett Co.**, north-facing bluff of Wolf River, 3 May 1984, *G. L. Walker, E. E. C. Clebsch, Z. E. Murrell 017* (TENN); 10. KENTUCKY, **Edmonson Co.**, mesophytic woods beside Bylew Ck., 7 June 1968, *K. A. Nicely and H. W. Elmore 1718* (UNC); 11. INDIANA, **Floyd Co.**, shale knobs, 18 May 1963, *A. C. Koelling 1065* (TENN); 12. TENNESSEE, **Cocke Co.**, roadside near Douglas Lake, 3 May 1966, *B. Allen s.n.* (TENN); 13. ALABAMA, **Colbert Co.**, rich north-facing slope over sandstone, 24 May 1974, *R. D. Whetstone and T.*

Table 5. ANOVA comparisons of pollen diameters (microns) between anther whorls within style morphs of *Oxalis grandis*. *n* = number of anthers sampled.

Morph	Anther Whorl	*n*	Mean	*F*	*P*
		Iron Mountain Gap			
Short	mid	2	35.45	0.07	0.80
	long	3	34.91		
Mid	short	6	29.85	0.22	0.65
	long	6	30.53		
Long	short	12	32.90	1.70	0.21
	mid	11	31.42		
		Watauga River			
Short	mid	1	41.60	NA	—
	long	2	37.12		
Mid	short	2	39.81	5.20	0.11
	long	3	35.54		
Long	short	4	34.14	2.01	0.19
	mid	6	35.41		

cence that he assumed arose from environmental and soil factors. The exception, *O. europea* Jord. (= *O. stricta* L.), had stem and pedicel pubescence that Wiegand attributed to the environment, but on the basis of geographical correlates, he postulated that hairiness on the abaxial leaf surface represented racial differentiation. In the most recent and thorough treatment of the section, Eiten (1963) contradicted Wiegand's views and relied upon variability in pubescence as a key diagnostic character in dividing section Corniculatae DC into subsections Corniculatae and Strictae Eiten. The diagnostic characteristics of the latter subsection were (i) the presence of septate hairs on stems, petioles and pedicels, and (ii) stems that arose singly from thin underground rhizomes (Eiten, 1963).

In contrast to our observations, prior studies have concluded that leaf hairs in *Oxalis grandis* are rare. Wiegand's (1925) description of *O. grandis* included presence of sparing pubescence

←

Atkinson 3198 (UNC); 14. TENNESSEE, Sinking Creek, moist woods, 11 June 1955, *J. Pearman s.n.* (EAST TENNESSEE STATE UNIVERSITY); C1. TENNESSEE, **Washington Co.**, shale; open woods, shale barren-like,16 May 1990, *K. Renzaglia s.n.* (VPI); C2. TENNESSEE, **Washington Co.**, Watauga Flats, 5 May 1978, *T. Bruce s.n.* (EAST TENNESSEE STATE UNIVERSITY).

Table 6. ANOVA comparisons of pollen diameters (microns) among style morphs of *Oxalis grandis* with SNK comparisons of mean diameters. Means followed by the same superscript were not significantly different ($P < 0.05$).

Iron Mountain Gap				
Source	df	MS	*F*	*P*
Among morphs	2	74.69	9.83	0.0003
Error	43	7.60		

Morph	*n*	Mean
Short	11	35.25[a]
Long	12	32.19[b]
Mid	23	30.19[b]

Watauga River				
Source	df	MS	*F*	*P*
Among morphs	2	19.85	4.44	0.03
Error	15	4.47		

Morph	*n*	Mean
Short	3	38.61[a]
Mid	5	37.25[a,b]
Long	10	34.91[b]

on the stems, villous petioles and peduncles, and glabrous leaves except for a few hairs on the underside; he did not distinguish septate from nonseptate hairs. Similarly, in an exhaustive study of section Corniculatae, Lourteig (1979) concluded that pubescence is rarely found on the leaf blades in *O. grandis*. Both studies noted a specimen (Cincinnati, C. G. Lloyd, 1882) that was unusually hairy on the stem with strigose abaxial leaf surfaces. Our results indicate that leaf blade pubescence occurs sporadically throughout the range of the species because nonseptate hairs were seen on abaxial leaf surfaces in 16 of 174 herbarium specimens examined.

Our results suggest that in *Oxalis grandis*, four different types of pubescence characters contribute to the extremely hirsute phenotype—an increase in the number of (1) septate and (2) nonseptate hairs, (3) elongation of both types of hairs throughout the vegetative axis and leaves, and (4) reorientation of hairs from appressed to patent. All except the last of these distinguishing characteristics are quantitative, and in only one of these (length of nonseptate hairs on the vegetative axis) is the extreme phe-

notype (long hairs) restricted to the Watauga River population. For the remaining quantitative characters, intermediate and extreme phenotypes occur either as isolated characters, or in various combinations.

Long, nonseptate hairs on stems occurred only in the Watauga River population (Table 4, StHrNS, specimens C1, C2). Considering the sample of herbarium specimens, there were no correlations involving the other two hair-length characters (LfHr; StHrS). However, in individual specimens, these two characters occurred singly (Table 4, specimen #4), in combination with each other (Table 4, specimen #12), or in various, apparently random combinations with other characters. From the apparent independence of these characters, we conclude that the hair length component of the Watauga River phenotype is a complex character.

In the screened herbarium sample, none of the character correlations involving septate hairs was significant. Nevertheless, the hirsute (Watauga River) phenotype was observed in eight specimens for number of septate hairs on petioles, six specimens for number of septate hairs on upper stems, and six specimens for number of septate hairs on lower stems (data not shown). In two specimens (Table 4, specimens #10, #13), septate hairs were absent on the upper stem, indicative of an extreme Iron Mountain Gap phenotype, but the number of nonseptate hairs was clearly typical of the Watauga River phenotype. In other herbarium specimens, nonseptate hairs were sparse (Iron Mountain Gap phenotype) but septate hairs were abundant (Watauga River phenotype) in corresponding regions of the plants. Two lines of evidence suggest that an increased number of septate hairs is independent of other pubescence characters. First, there were no significant character correlations involving septate hairs in the herbarium sample. Second, hirsuteness for septate hairs occurred in combination with extreme variation (encompassing both phenotypes) in the numbers of nonseptate hairs.

In the herbarium sample, there were no obvious ecological or geographical correlates associated with the occurrence of pubescent plants. Because herbarium sheets rarely contain more than a few individual plants, it is not possible to know if pubescent plants represent unusual plants or if, like the Watauga River population, the entire population is fixed for some increased degree of hairiness. Nevertheless, the observation that plants representing both extremes of hairiness retained their characteristic phe-

notypes after propagation in a common environment indicates a genetic basis (Levy and Moore, 1993).

Although character correlations exist within the Iron Mountain Gap sample (Table 4), these plants showed little tendency toward the hirsute phenotype. Therefore, the meaning of these particular correlations is unclear. The Watauga River population provided the standard by which we defined the extreme hirsute phenotype with multiple positive associations among pubescence characters. However, the sample of selected herbarium specimens may provide a key to understanding the complexity of pubescence in *Oxalis grandis*. These specimens were selected because each showed a tendency towards hairiness. Within this sample, all characters involving nonseptate hairs were positively correlated, suggesting simple genetic control may underlie the increased number of nonseptate hairs. On the other hand, numbers of septate hairs appeared independent of all other characters, and therefore is probably under independent genetic control. Furthermore, neither of the two hair-number characters were correlated with increased length of either type of hair.

If one considers only qualitative differences between phenotypic extremes (e.g., patent versus appressed hairs; short versus long nonseptate hairs), then it could be concluded that pubescence is a simple character. For example, in *Dithyrea* (Rollins, 1958) and *Linum* (Rogers, 1968) hairiness is controlled by a single genetic locus. However, in *Oxalis grandis* we have provided several lines of evidence involving qualitative as well as quantitative pubescence attributes suggesting a more complex character. In the herbarium sample we found (i) only one significant character correlation in common with the Watauga River population, (ii) no significant correlations between septate and nonseptate hairs and, (iii) no individuals with long nonseptate hairs on stems or petioles (unlike their ubiquitous occurrence in Watauga River). The apparent complexity of the pubescence character in *Oxalis grandis* endows it with significant value as an indicator of taxonomic relationship but, the contrast between *Dithyrea* and *Oxalis* highlight the necessity of a detailed character analysis for each taxon under study.

POLLEN SIZE. Citing data from his own crosses, as well as from Muller and Hildebrand, Darwin (1877) convincingly showed that illegitimate pollination of several heterostylous *Oxalis* species resulted in dramatically reduced seed production compared

to legitimate pollinations. In *O. regnellii, O. speciosa,* and *O. valdiviana,* pollen diameter was correlated with the stamen whorl from which it was produced. The largest grains were produced in long stamens, whether these stamens occurred on short- or mid-styled flower morphs; the smallest pollen was found in short anthers. Pollen in *Oxalis grandis* also is heteromorphic. In both populations of *Oxalis grandis* examined, short-styled morphs produced the largest pollen (Table 5). However, pollen diameter in this tristylous species is largely a function of the style morph on which it was produced; pollen from different anther whorls within a style morph are similar in size.

Several heterostylous species in *Oxalis* subsection Corniculatae have lost the self-incompatibility response and others show evidence of loss of intermorph morphological differences (Ornduff, 1972). The three closely related species that constitute *Oxalis* subsection Strictae (*O. grandis, O. stricta, O. suksdorfii*) are all moderately to strongly self-compatible (Ornduff, 1964, 1972). Moreover, pollen size in this section of the genus is not clearly related to the length of the anther whorl. For example, long anthers on short- and mid-styled morphs in *O. suksdorfii* produced the largest pollen, but there was no difference in pollen size between anther whorls in long-styled morphs. The size of pollen grains from corresponding anthers on different style morphs differed within long and mid anther whorls (Ornduff, 1964). Mid-styled flowers showed strong pollen size differences between anther whorls that was accompanied by physiological differences in the incompatibility reaction (Ornduff, 1964).

In some species of *Oxalis,* differences in pollen size have been noted between populations as well as among anther whorls. For example, pollen diameter differed among anther whorls from two style morphs within each of three populations of *O. dillenii* ssp. *filipes,* but the morph that lacked pollen size differentiation among anther whorl types was not the same in each population (Ornduff, 1972). *Oxalis alpina* (section Ionoxalis) consists of di- and tristylous populations. In the former, style morphs clearly differed in the size of pollen produced, but there were no size differences among anther whorls within style morphs (Weller, 1976). Pollen appeared trimorphic in tristylous populations, but the magnitude of differences between morphs was not as pronounced as in distylous populations (Weller, 1976). A detailed analysis of the trimorphic pollen of *Oxalis pes-capre* showed variation among

populations when pollen from equivalent anthers was compared (Ornduff, 1987). In the present study, pollen size was remarkably different between the Watauga River and Iron Mountain Gap populations within each flower morph. Pollen from the Watauga River population always is larger and, for the mid- and long-styled morphs, these differences are highly significant.

CONCLUSIONS

Two lines of evidence suggest that, in *Oxalis grandis,* pubescence is genetically controlled. In prior studies, distinct pubescence phenotypes retained their respective suites of characteristics in a common environment. The current study uncovered the sporadic occurrence of plants with varying degrees of a pubescent phenotype, but these plants did not share obvious geographical or ecological factors. Furthermore, the correlation analysis has shown that components of pubescence vary independently in nature. While a determination of the genetic basis of pubescence is premature without a formal genetic analysis, the current findings suggest a genetic architecture more complex than a single locus. We postulate that the constellation of characters leading to an extremely pubescent phenotype may arise from either the combined actions of a minimum of three loci with major effects or it may result from several polygenic characters. The complexity of the phenotype tends to lend credence to Eiten's emphasis on pubescence as a diagnostic character in *Oxalis* section Corniculatae.

Copious, long patent hairs and relatively large pollen grains indicate the Watauga River population is an extreme variant of *Oxalis grandis.* This population also differs in other attributes from more typical representatives of the species. For example, there were distinct differences from the Iron Mountain phenotype with respect to the pattern of its circadian rhythm of leaflet sleep movements as well as its responses to light level fluctuations (Levy and Moore, 1993) which suggest some fundamental physiological diversity. Finally, the Watauga River population occupies an unusual habitat—steep slopes underlain by easily eroded shale of the Sevier formation. The resultant substrate and habitat is reminiscent of the shale barrens of Virginia and West Virginia. These sites are known to support regionally rare species and some areas recently have been afforded protection. Future studies may show

that the extremely pubescent phenotype is worthy of varietal status but, for the present, we have chosen to adopt a conservative approach and retain *Oxalis grandis* as a monotypic species but to recognize its morphological and physiological diversity.

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DEPARTMENT OF BIOLOGICAL SCIENCES
EAST TENNESSEE STATE UNIVERSITY
JOHNSON CITY, TENNESSEE 37614

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FLORISTIC DIVERSITY OF A DISTURBED WESTERN OHIO FEN

JAMES S. MCCORMAC AND GREGORY J. SCHNEIDER

ABSTRACT

During the 1990–1992 growing seasons vegetation was surveyed in a Logan County, Ohio fen. This 23 ha site was subjected to intense substrate disturbance resulting from peat mining activities which took place from 1980 to 1985. Thousands of cubic meters of peat and marl were removed from the fen and virtually the entire surface area was affected by dredging activities. Surveys of the fen prior to mining indicate that the site was occupied mostly by shrub communities dominated by *Cornus* spp., *Rosa palustris,* and other woody species. However, shrubs are infrequent at the present time. Post-disturbance surveys documented a total of 208 vascular plant taxa, including 22 species listed as rare in Ohio. Several species are present which are disjunct from areas in the state where they normally occur, or are not known elsewhere in western Ohio.

Key Words: bog fen, disjuncts, peat mining, prairie fen, rare plants, substrate disturbance

INTRODUCTION

Fens are alkaline peatlands which survive as relict wetland communities scattered throughout glaciated Ohio. Prior to European settlement, peatlands were estimated to cover 74,000 ha in Ohio (Dachnowski, 1912). Recent work by Andreas and Knoop (1992) indicates that approximately 98% of the state's peatlands have been destroyed. The primary cause of this loss has been conversion of land for agricultural purposes, accounting for 85% of the total loss of peatlands. Additional factors contributing to the disappearance of these wetlands are recreation (vacation cottages, camps, etc.), modification of hydrology, mining and other development. Other more insidious factors causing a decrease in diversity and an eventual elimination of typical fen associations are natural succession into woody plant communities and invasion by non-native plants. Alien species, in particular *Rhamnus frangula* L. (European Buckthorn), have detrimentally impacted many of Ohio's fens. Left unchecked, this species can proliferate to the point of eliminating much of the native flora.

Numerous rare plant taxa, and a few species of rare animals, are confined to or exist primarily in fens in Ohio. Many of the plants require the combination of marl (calcium carbonate pre-

cipitate derived from artesian spring waters) substrate, cool subsurface soil temperatures, and saturated soil conditions. Most of the species which are exclusive to fens in Ohio occur in a wider variety of habitats elsewhere. In Ohio, many of these species are on the edge of their range, and therefore require the specialized combination of habitat parameters in fens to gain a competitive advantage over more generalized wetland species which are unable to tolerate the harsh conditions within fens. Rare plants exclusive to fens in Ohio include: *Carex flava* L., *Carex sterilis* Willd., *Cladium mariscoides* (Muhl.) Torr., *Eleocharis pauciflora* (Lightf.) Link., *Eriophorum viridicarinatum* (Engelm.) Fern., *Triglochin maritimum* L., *Triglochin palustre* L., *Tofieldia glutinosa* (Michx.) Pers., *Zigadenus elegans* Pursh var. *glaucus* (Nutt.) Preece, *Cypripedium calceolus* L. var. *parviflorus* (Salisb.) Fern., *Spiranthes romanzoffiana* Cham., *Deschampsia caespitosa* (L.) P. Beauv., *Cacalia plantaginea* (Raf.) Shinners, *Solidago ohioensis* Riddell, *Utricularia cornuta* Michx., *Myrica pensylvanica* Mirbel., *Salix myricoides* (Muhl.) J. Carey, and *Valeriana edulis* Nutt. var. *ciliata* (T. & G.) Cronq. (Anon., 1992). Uncommon animals often found in fens include *Clemmys guttata* Schneider (Spotted Turtle) and *Sistrurus catenatus* Rafinesque (Massasauga Rattlesnake).

STUDY AREA

The study site, known as McCracken Fen, is located in west-central Ohio near the city of Bellefontaine, county seat of Logan County (Figure 1). This region is characterized by low, rolling hills formed by a series of kames and eskers deposited by the Wisconsin ice sheet. McCracken Fen is situated on a large terminal moraine which spans most of Logan County. Artesian springs which emanate from deep gravel deposits are frequenct in this area, as evidenced by names of local towns; Bellefontaine (French for beautiful fountain), Big Springs, and Springhills. The abundance of springs had led to the formation of numerous fens in the Champaign-Clark-Logan county region (Schneider, 1992), although many of these now have been destroyed (Andreas and Knoop, 1992).

McCracken Fen is situtated in a bowl-like depression surrounded by rather abruptly sloping gravel ridges on three sides. The south side is bordered by a small tract of Elm-Ash swamp forest which grades into agricultural fields. The fen was mined for peat

Figure 1. Location of McCracken Fen, Logan County, Ohio.

and marl products over a period of approximately five years, beginning in 1980. Many tons of substrate were removed from nearly all areas of the peatland. This dredging caused intensive disturbance to the surface of the wetland, and is still obvious in the form of ditches, furrows, open flats, and artificial deepwater pools (Figure 2). In 1985, the mining company apparently went bankrupt, and operations abruptly ceased. Heavy equipment such as draglines, cranes, tractors, and a small peat packaging plant were abandoned and are still present at the site.

The hydrology of the fen is maintained by artesian springs entering the wetland from the east. Although mining activities altered the natural openings of these springs, they continue to flow

Figure 2. Post-disturbance aerial photograph of McCracken Fen, Logan County, Ohio. Taken June, 1990, by ODNR.

at a rapid rate. Attempts to drain McCracken Fen via ditches and drainpipes were unsuccessful, as the volume of water entering the fen appears to have offset the amount which was drained off.

METHODS

Field surveys of McCracken Fen began in September of 1989. A chance visit to the site by McCormac resulted in the discovery of *Scirpus smithii* Gray (Smith's Bulrush), which at that time was known from only one small, possibly extirpated, population in Ohio. During 1990, 1991 and 1992, eleven collecting trips were made to the fen, between April and October. Two hundred and eight species of vascular plants were collected and voucher specimens were deposited in the following herbaria: CLM, KE, MICH, MU, and OS (Holmgren et al., 1990). An effort was made to record frequency and abundance of all plant taxa, based on field observations, and using codes supplied by Reznicek and Catling (1989). Detailed information regarding plants listed as rare in Ohio (Anon., 1992) is on file in the Ohio Natural Heritage database.

Standard regional manuals were used for identification of spec-

imens, particularly Fernald (1950), Gleason and Cronquist (1991), and Voss (1972, 1985). Nomenclature follows Gleason and Cronquist (1991).

RESULTS AND DISCUSSION

Rare Plants. Of the 208 species of vascular plants collected in McCracken Fen, one is considered endangered in Ohio, seven are threatened, and fourteen are potentially threatened (Anon., 1992).

Many of these species are rare in Ohio due to their specificity of habitat, and the majority are obligate fen species. As most of the state's original fen communities have been destroyed or greatly altered, many of the plants typically associated with this type of wetland have become rare and local. Rare species are placed into categories based on guidelines established by the Division of Natural Areas and Preserves (Anon., 1992). Species classified as endangered in Ohio are restricted in distribution to an area delineated by three or fewer U.S. Geological Survey 7.5 minute topographic maps. Threatened species occur on between four and seven quadrangle maps or have fewer than ten total populations statewide. Potentially threatened species are believed to be declining in abundance in Ohio and have been placed in this "watch" category due to their dependence on fragile ecosystems which have become increasingly rare.

The presence of species with "threatened" (T) and "endangered" (E) status in McCracken Fen is noteworthy, and these plants are discussed individually below:

Betula pumila L. (T): This northern shrub is known from only six extant populations in Ohio, mostly in the northern part of the state. The nearest population to McCracken fen is at Cedar Bog in adjacent Champaign County, a well-studied site (Frederick, 1974) which is floristically similar to McCracken Fen.

Carex bebbii (L.H. Bailey) Fern. (T): Another northern species known from ca. eight sites in northern Ohio, most of which are on the lake plain of Lake Erie. The McCracken Fen population is disjunct from the nearest Ohio site by 120 km, and is one of the most southerly populations in the midwest.

Carex sartwellii Dewey. (T): This plant is known from about ten sites in Ohio, mostly in the western half of the state. Many years these populations remain largely sterile, thus rendering de-

tection difficult. Field observations by the authors in recent years suggest that fire, and possibly other forms of disturbance, may induce flowering.

Eleocharis flavescens (Poiret) Urban, var. *olivacea* (Torr.) Gleason. (T): This species is very habitat specific in Ohio, as all eight extant populations occur in seasonally exposed, saturated peat, usually on the drying shores of lakes or ponds. With the exception of a site in Champaign County, the nearest population to McCracken Fen is ca. 130 km to the north.

Pogonia ophioglossoides (L.) Ker Gawler. (T): This was one of the most exciting discoveries, as this orchid was reported only once before on the till plains of western Ohio, from a peat bog which straddled the Champaign-Logan county line and has since been destroyed. Only five small populations of Rose Pogonia are known to be extant in Ohio, primarily in the northeastern quarter of the state.

Scirpus smithii A. Gray. (E): One of the rarest plants in Ohio, Smith's Bulrush was known from only one site in Ohio, on the shore of Lake Erie in Ottawa County. The plant has not been seen at the Lake Erie site in recent years; therefore, the McCracken Fen population may be the only extant site in Ohio. It should be noted that we treat *Scirpus smithii* A. Gray and *S. purshianus* Fern. as distinct species; Ohio material of the former is easily separated from the latter. Gleason and Cronquist (1991) submerge these taxa under the name *Scirpus smithii.*

Sphenopholis obtusata (Michx.) Scribn. var. *obtusata* (T): Currently known from only five sites in Ohio, most records of this easily overlooked and/or misidentified species are from the western half of Ohio.

Utricularia intermedia Hayne. (T): Eight populations are known in Ohio, from glacial lakes in northern Ohio, and saturated marly ground of a few fens in west central Ohio.

Aliens. Non-native species accounted for 8% of the vascular flora of McCracken Fen, or 18 species. However only two of these, *Rhamnus frangula* and *Solanum dulcamara* L. have become established within the fen, although they are not yet common. The remaining alien species persist locally in the transition zone between upland and fen, or are occasional on drier hummocks in the fen. Whereas non-native plants are well-known colonizers of disturbed ground (Muenscher, 1935), the low incidence of aliens in the flora of McCracken Fen, in spite in the recent heavy dis-

turbance, may be attributable to three factors. The substrate of fens are consistently low in temperature, low in oxygen availability, and are nutrient deficient (Van der Valk, 1977). These factors create an environment suitable only for an assortment of plants which have adapted to these conditions, and may account for the relative lack of colonization by non-native species.

Disjuncts. Many species in the flora of McCracken Fen are of a northern and/or coastal plain affinity. A number of these plants reach the southern limits of their range in Ohio in the extreme northern and northeastern sections of the state, and also occur sparingly as disjuncts in the fens and bogs of central Ohio. Examples of this type of distribution which are found at McCracken Fen include *Betula pumila, Carex bebbii, Eleocharis flavescens* var. *olivacea, Eriophorum viridicarinatum, Rhynchospora alba* (L.) Vahl., *Scirpus smithii,* and *Utricularia intermedia* (Figure 3).

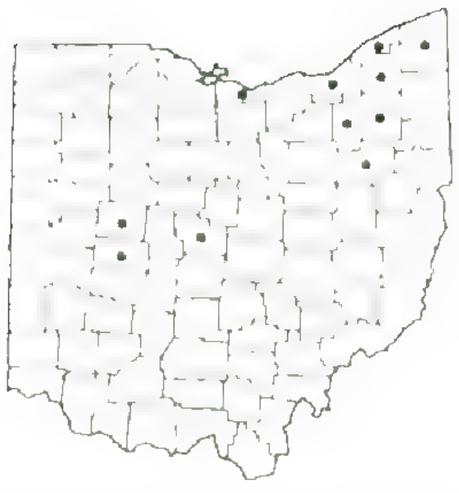
PRE-DISTURBANCE PLANT COMMUNITIES

Information regarding the condition of McCracken Fen prior to the mining operation is scarce; however the site was known to botanists and was visited several times. Pehaps the best documentation of pre-disturbance conditions are aerial photographs of the fen taken by the Ohio Department of Natural Resources (ODNR) in 1978 (Figure 4). These pictures indicate that the fen was largely vegetated by woody shrubs such as *Cornus* spp. and *Rosa palustris* Marshall. An extensive stand of *Scirpus acutus* Muhl. is also evident. When the 1978 photograph (Figure 4) is compared with a photo taken in 1992 (Figure 2), the change in composition of vegetation caused by the mining operating is evident.

Botanists Allison W. Cusick and Guy L. Denny, both employees of ODNR, also visited McCracken Fen in the mid-1970's, prior to mining. They state (pers. comm.) that the fen was practically impenetrable due to the dense shrub zones, and with the exception of *Potentilla fruticosa* L., no unusual or state-listed plants were observed.

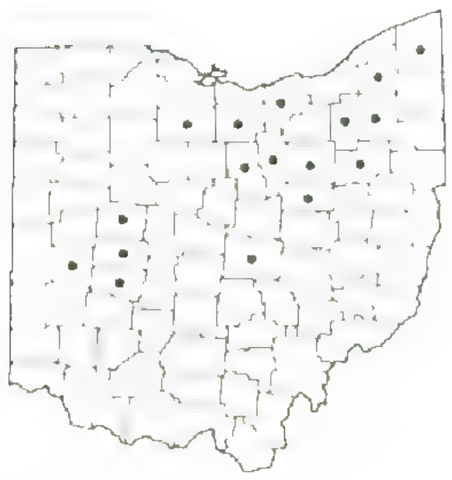
POST-DISTURBANCE PLANT COMMUNITIES

Six distinct zones of vegetation exist in present-day McCracken Fen. With the exception of the open water habitat, and weedy



Eriophorum viridicarinatum

Scirpus smithii



Rhynchospora alba

Utricularia intermedia

Eleocharis flavescens var. olivacea

Betula pumila

Carex bebbii

Figure 3. Ohio distribution of species which occur as disjuncts in western Ohio fens, including McCracken Fen, Logan County, Ohio.

peripheral zone, these vegetation zones resemble those which occur naturally in many other undisturbed Ohio fens. As these zones were artifically created as a side-effect of the peat-mining operations, they differ in some respects from naturally occurring habitats. Within several of the zones there are also recognizable microhabitats.

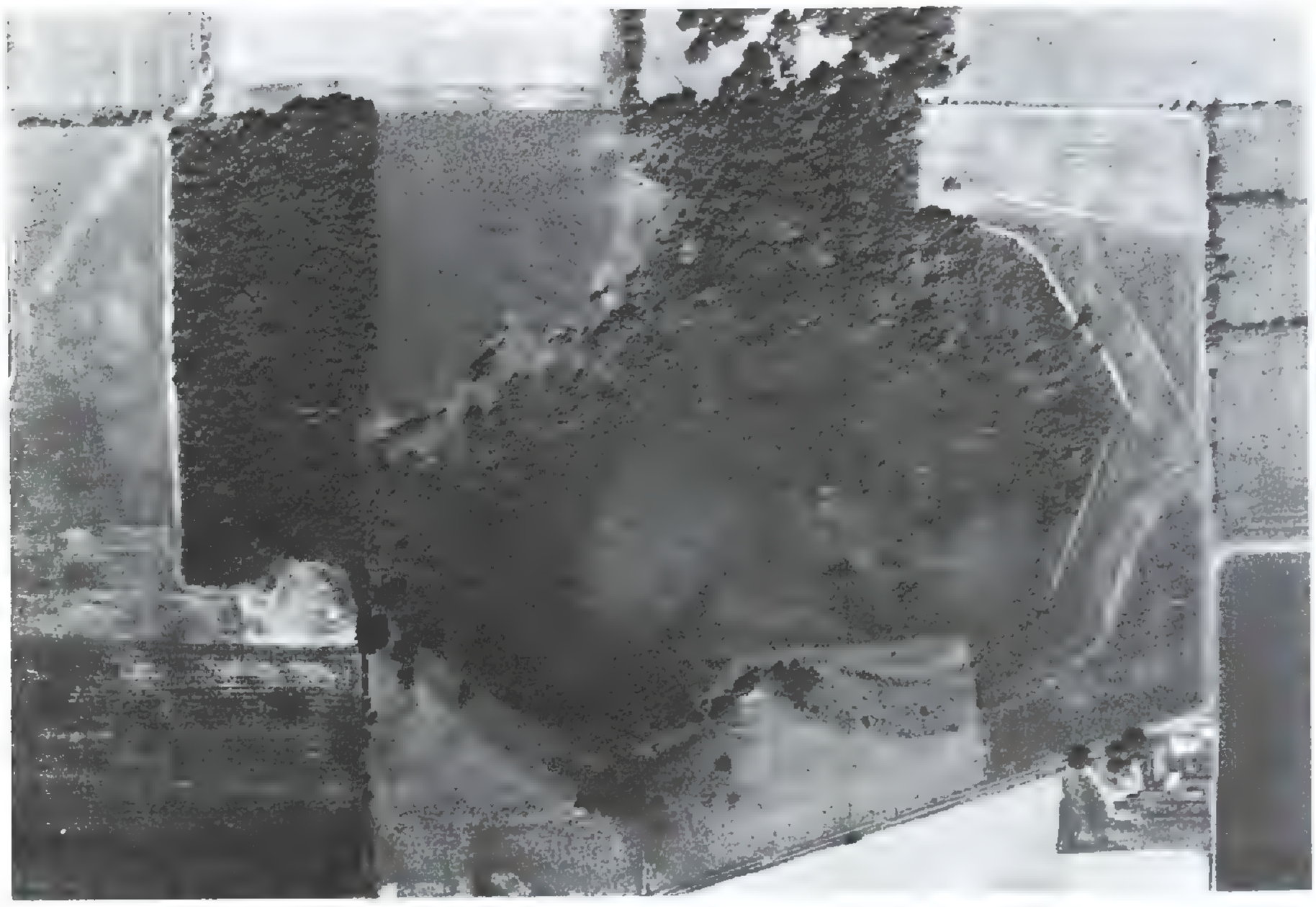


Figure 4. Pre-disturbance aerial photograph of McCracken Fen, Logan County, Ohio. Taken August, 1978, by ODNR.

Open Water Areas. This habitat shows the most visible effect of the mining activities. Two large areas, each ca. 1.5 ha in size, were dredged to a much greater depth than other areas of the fen, leaving ponds which vary from 30 cm to 5 m in depth. Fed by artesian springs, these ponds have exceptionally clear water and support twelve species of aquatic plants, as well as a number of species dependent on the open, marshy ground bordering the ponds. It is interesting that the composition of flora inhabiting the open water areas is similar to that which is found in nearby glacial lakes. In addition to the two large ponds, a number of much smaller open water areas exist in the fen, usually in the form of deeply dredged ditches.

Aquatic plants characteristic of the open water habitat include *Brasenia schreberi* J.F. Gmelin, *Lemna minor* L., *Najas flexilis* (Willd.) Rostkov & Schmidt, *Nuphar advena* (Aiton) Aiton f., *Nymphaea odorata* Aiton, *Potamogeton illinoensis* Morong, *P. pectinatus* L., and *Utricularia vulgaris* L.. Species typical of saturated open soil bordering water areas include *Alisma subcordatum* Raf., *Carex comosa* F. Boott., *C. lurida* Wahlenb., *Eleocharis palustris* L., *Eupatorium perfoliatum* L., *Leersia oryzoides*

(L.) Swartz, *Mimulus ringens* L., *Sagittaria latifolia* Willd., *Scirpus acutus,* and *Verbena hastata* L.

Marl Flats. Open marl flats provide habitat for some of the rarest obligate fen plants in Ohio. Marl flats are invariably associated with outflows of spring water containing calcium and magnesium salts. These water-borne minerals precipitate after reaching the surface and combine with peat to form a substratum of marl throughout the fen.

Water flow through McCracken Fen has been altered to the point where naturally forming marl flats are not present. However, marly peat flats have been created by the peat excavating process. In several areas, small flats were created when the overlying peat layer was removed, exposing the underlying marl. These artificial marl flats are saturated to the surface by ground water, and are habitat for an unusual assortment of plants, including many rare or uncommon species. Plant taxa typical of the marl flats include *Cyperus bipartitus* Torr., *C. flavescens* L., *Eleocharis tenuis* (Willd). Schultes var. *borealis* (Svenson) Gleason, *Fimbristylis autumnalis* (L.) Roemer & Schultes, *Hypericum majus* (A. Gray) Britton, *Juncus articulatus* L., *J. brachycephalus* (Englem.) Buchenau, *J. canadensis* J. Gay., *J. nodosus* L., *Rhynchospora alba, R. capillacea* Torr., *Scleria verticillata* Muhl., and *Spiranthes cernua* (L.) Rich. Noteworthy is the almost complete dominance of two families, the Cyperaceae and Juncaceae. The frequency of these two groups in soils that were heavily disturbed by mining activities suggests a strong capability to store seeds in a viable state for an extended period deep within the substratum.

Another type of flat occurs within McCracken Fen and is quite different in composition of substrate and cause of origin, than the above described marl flats. Autumnally exposed flats occur along the margins of the open water areas, due to a slight (±15 cm) drop in water levels, which begin to recede in mid-summer. By September these areas are fully exposed. The substrate of these shoreline flats is composed of unconsolidated, saturated peat which is very unstable, and low in diversity of flora. However, two of the rarest species present in the fen, *Eleocharis flavescens* var. *olivacea* and *Scirpus smithii,* occur in this habitat. Other species commonly found in this zone are: *Bidens cernua* L., *Cyperus odoratus* L., and *Ludwigia palustris* (L.) Elliott.

Potentilla Fruticosa Meadow. This is the largest plant community in the fen, occupying ca. 5 or 6 ha. This habitat appears

to be nearly a monoculture of *Potentilla* when viewed from a distance, although it is easily the most diverse zone in McCracken Fen. Slight changes in moisture regime influence supporting vegetation, as does the presence of *Sphagnum*. The driest areas of the meadow are relatively low in species diversity, while wetter areas support an impressive array of plants. Some of the dominant species in this community include *Aster puniceus* L., *A. umbellatus* Miller, *Campanula aparinoides* Pursh, *Cladium mariscoides, Eupatorium maculatum* L., *Galium tinctorium* L., *Lobelia kalmii* L., *Muhlenbergia glomerata* (Willd.) Trin., *Potentilla fruticosa, Scutellaria lateriflora* L., *Solidago ohioensis, S. patula* Muhl., *S. rugosa* Miller, *Thelypteris palustris* Schott., and *Toxicodendron vernix* (L.) Kuntze.

One small section in the wettest area of the *Potentilla* meadow contains a lush growth of *Sphaghum* sp., and harbors several vascular plants found nowhere else in McCracken Fen. These are *Calopogon tuberosus* (L.) BSP., *Drosera rotundifolia* L., *Epilobium leptophyllum* Raf., *Eriophorum viridicarinatum,* and *Pogonia ophioglossoides.*

Graminoid Meadow. This is the rarest vegetation zone, occupying only a small (<5%) area of the total fen. Two different types of meadow are present, one dominated by grass (Poaceae) and the other composed primarily of sedges (Cyperaceae). The grass dominated meadow is ca. 0.4 ha in size, and is a virtual monoculture of *Calamagrostis stricta* (Timm.) Koeler. Species diversity in this meadow is quite low.

The sedge meadows are quite small, averaging only a few square meters. These occur primarily within the *Potentilla fruticosa* meadow, as small, randomly scattered openings. The dominant species found in the sedge meadows include *Aster borealis* Prov., *Carex flava, C. interior* L. Bailey, *C. leptalea* Wahlenb., *Epilobium coloratum* Biehler, *Scutellaria galericulata* L., and *Triadenum fraseri* (Spach) Gleason.

Shrub Zone. In contrast to conditions in the fen prior to mining, shrub zones now cover a relatively small area. Two distinct areas of this habitat, covering ca. 3–4 ha, are present. One of the shrub zones is dominated primarily by *Cornus amomum* Miller and *Rosa palustris.* This area is one of the least diverse habitats in the fen, as the dense, virtually impenetrable thickets exclude most herbaceous growth. The other shrub zone is dominated by a variety of woody species and shade tolerant herbaceous plants.

Dominant woody species include *Betula pumila, Cornus amomum, Fraxinus pennsylvanica* Marshall, *Ilex verticillata* (L.) A. Gray, *Populus deltoides* Marshall, *Rosa palustris, Salix discolor* Muhl., *S. sericea* Marshall, and *Ulmus rubra* Muhl. The understory herbaceous stratum of this thicket is quite diverse. Some of the dominant species include *Agrimonia parviflora* Aiton, *Aster lateriflorus* (L.) Britton, *Boehmeria cylindrica* (L.) Swartz, *Clematis virginiana* L., *Cuscuta gronovii* Willd., *Galium tinctorium, Glyceria striata* (Lam.) A. Hitchc., *Impatiens capensis* Meerb., *Onoclea sensibilis* L., *Osmunda regalis* L., and *Solidago gigantea* Aiton.

Weedy Peripheral Zone. Few non-native plant species have attained a foothold within McCracken Fen, the two notable exceptions being *Rhamnus frangula* and *Solanum dulcamara.* As most of the perimeter of this fen grades abruptly into dry, gravelly slopes, much of which has been disturbed by mining activities, there exists a narrow zone characterized by non-native species bordering the fen. Most of these alien plants do not penetrate far into the fen, and for the most part, do not occur in heavy concentrations. Two species which have become locally abundant in wetter areas of this zone are *Phalaris arundinacea* L. and *Typha angustifolia* L.

Some of the more common non-native plants occurring in the weedy peripheral zone include *Achillea millefolium* L., *Brassica nigra* L., *Chrysanthemum leucanthemum* L., *Convolvulus arvensis* L., *Daucus carota* L., *Nepeta cataria* L., and *Setaria viridis* (L.) P. Beauv.

FLORISTIC COMPARISON WITH OTHER OHIO FENS

Stuckey and Denny (1981) analyzed the floristic affinities of Ohio's fens. They concluded that two distinctive types of fens occurred in the state. They used the term prairie fen to describe fens in west-central and south-central Ohio. These fens have a distinctive floristic affinity with the wet, tall-grass prairies of the midwestern United States. The term bog fen was introduced to describe fens which occur in northeastern and extreme northwestern Ohio. These fens share many species with Ohio's kettle bogs. These species have northern affinities and are often abundant in the boreal fens of northern Michigan, northern Minnesota and Canada. Stuckey and Denny (1981) recognized that Cedar

Bog, a fen in west-central Ohio, was unique to the state in that its flora included both the prairie and boreal elements. McCracken Fen, which is located 32 km north of Cedar Bog, was relatively unknown until recently and was not discussed by Stuckey and Denny. This fen has some of the boreal species which otherwise occur mostly in northern fens or at Cedar Bog. These species include *Betula pumila, Eriophorum viridicarinatum, Rhynchospora alba* and *Pogonia ophioglossoides.* Another interesting facet of McCracken Fen's flora is the absence of many of the species of wet prairie affinity which are so characteristic of all of the other fens in this part of the state. Examples of species typical of Ohio prairie fens which do not occur at McCracken Fen include *Andropogon gerardii* Vitman, *Cacalia plantaginea* (Raf.) Shinners, *Coreopsis tripteris* L., *Liatris spicata* (L.) Willd., and *Silphium terebinthinaceum* Jacq.

CONCLUSIONS

Although no thorough surveys were made of McCracken Fen prior to the mining operation, evidence strongly suggests that the study area was in an advanced state of succession. Pre-mining photographs and accounts of observers indicate that shrub zones blanketed most of the fen, greatly reducing diversity. Mining activities removed most of the shrub zones, as well as some of the substrate. During the mining process, soils in the fen were heavily disturbed by the heavy equipment used to excavate the peat. It would seem likely that the combination of eliminating most of the shrub zones, thus restoring open fen meadow/marl flat habitat, and stimulating the seedbank by disrupting the substrate, resulted in increased diversity. Many of the plant taxa now present in McCracken Fen are characteristic of fens in Ohio, yet it is unlikely that they colonized the site from outside sources, as there are no other fens in the immediate vicinity. The dramatic shift in vegetation resulting from the mining operation suggests that fen soils are capable of storing large, viable seedbanks, and that restoration of fens in advanced successional states is possible.

ANNOTATED LIST OF THE VASCULAR PLANTS OF MCCRACKEN FEN, LOGAN COUNTY, OHIO

All species included on this list are represented by voucher specimens deposited in herbaria, as indicated following each spe-

cies. Nomenclature and phylogenetic order follow Gleason and Cronquist (1991). Each species is assigned a frequency code, as follows: rare, occasional, or abundant; and local, scattered or widespread (Reznicek and Catling, 1989). Habitat(s) in which each species occurs is given, using the following abreviations: GM (Graminoid Meadows), MF (Marl Flats), OW (Open Water), PM (*Potentilla fruticosa* Meadow), SZ (Shrub Zones) and WP (Weedy Peripheral Zone). Finally, our collection numbers for all taxa are given. Superscripts preceding species' names indicate: 1, non-native; 2, endangered; 3, threatened; and 4, potentially threatened.

PTERIDOPHYTES

EQUISETACEAE

Equisetum fluviatile L.—Occasional and local in SZ (*3675* OS).

OSMUNDACEAE

Osmunda regalis L.—Occasional and scattered in SZ (*1692* OS; *2724* MU).

ASPLENIACEAE

Thelypteris palustris Schott.—Abundant and widespread in PM, GM, and SZ (*3181* OS).

Dryopteris cristata (L.) A. Gray—Occasional and local in SZ (*4065* MU).

ONOCLEACEAE

Onoclea sensibilis L.—Occasional and local in SZ (*3651* OS).

DICOTYLEDONS

NYMPHAEACEAE

Nuphar advena (Aiton) Aiton f.—Abundant and local in OW (*2415* MU, OS).

Nymphaea odorata Aiton—Abundant and local in OW (*2620* CLM).

CABOMBACEAE

Brasenia schreberi J.F. Gmelin—Occasional and local in OW (*2417* MU).

RANUNCULACEAE

Caltha palustris L.—Rare and local in SZ (*4525* CLM, MU).

Anemone virginiana L.—Rare and local in PM (*3917* KE).

Clematis virginiana L.—Occasional and local in SZ (*2880* MU, OS).

Ranunculus recurvatus Poiret—Rare and local in SZ (*3650* OS).

R. abortivus L.—Rare and local in SZ (*3649* OS).

BERBERIDACEAE

Podophyllum peltatum L.—Rare and local in SZ (*4527* MU).

PLATANACEAE

Platanus occidentalis L.—Rare and local in SZ (*3915* OS).

ULMACEAE

Ulmus rubra Muhl.—Occasional and local in SZ (*3666* OS).

URTICACEAE

Urtica dioica L. var. *procera* (Muhl.) Wedd.—Occasional and scattered in WP (*3173* OS).

Boehmeria cylindrica (L.) Swartz—Occasional and scattered in OW, PM, and SZ (*3179* MU).

Pilea pumila (L.) A. Gray—Occasional and local in SZ (*3182* OS).

BETULACEAE

[3]*Betula pumila* L.—Occasional and local in PM and SZ (*2616* CLM, OS).

PORTULACACEAE

Claytonia virginica L.—Rare and local in SZ (*4528* MU).

POLYGONACEAE

[1]*Rumex crispus* L.—Rare and local in WP (*3671* OS).

Polygonum lapathifolium L.—Occasional and scattered in OW, WP (*3165* OS, *3347* OS).

P. pensylvanicum L.—Occasional and scattered in OW (*3162* OS).

[1]*P. hydropiper* L.—Rare and local in OW (*3190* OS).

P. punctatum Elliott—Occasional and scattered in OW (*3050* OS).
[1]*P. persicaria* L.—Rare and scattered in OW and WP (*3049* OS).
P. sagittatum L.—Occasional and scattered in SZ (*3174* MU).
P. scandens L.—Rare and local in SZ (*3049* OS).

CLUSIACEAE

Hypericum punctatum Lam.—Rare and local in MF (*2883* OS; *3028* OS).
H. multium L.—Occasional and local in MF (*1694* KE; *2876* MICH; *3029* MICH).
[4]*H. majus* (A. Gray) Britton—Occasional and local in MF (*2877* MICH; *3043* OS).
Triadenum fraseri (Spach) Gleason—Occasional and scattered in GM, OW, and PM (*1684* OS).

DROSERACEAE

[4]*Drosera rotundifolia* L.—Occasional and local in PM (*2611* OS).

VIOLACEAE

Viola sororia Willd.—Occasional and scattered in PM, SZ, and WP (*4535* MU).
V. macloskeyi F. Lloyd—Occasional and local in SZ (*4526* KE, MU).

SALICACEAE

Populus grandidentata Michx.—Rare and local in SZ (*2614* OS).
P. deltoides Marshall—Occasional and scattered in SZ and WP (*3643* OS).
Salix amygdaloides Andersson—Rare and local in WP (*3645* OS).
S. lucida Muhl.—Occasional and local in SZ (*3674* MU).
S. exigua Nutt.—Occasional and local in SZ and WP (*2617* MU; *3644* OS).
S. sericea Marshall—Occasional and local in SZ (*3655* OS).
S. discolor Muhl.—Occasional and local in SZ (*3191* OS; *3656* CLM).

BRASSICACEAE

[1]*Brassica nigra* L.—Rare and local in WP (*4785* MU).

Rorippa palustris (L.) Besser—Rare and local in MF (*4769* MU).

PRIMULACEAE

Lysimachia quadriflora Sims.—Abundant and widespread in GM, MF, and PM (*4766* MU).

L. thyrsiflora L.—Rare and local in SZ (*2420* KE).

GROSSULARIACEAE

Ribes americanum Miller—Occasional and local in SZ (*3661* OS; *4529* MU).

SAXIFRAGACEAE

Penthorum sedoides L.—Occasional and scattered in GM, OW, and PM (*3164* OS).

ROSACEAE

Fragaria virginiana Duchesne—Rare and local in WP (*4531* MU).

Potentilla norvegica L.—Rare and local in WP (*3654* OS; *3916* KE).

P. fruticosa L.—Abundant and local in PM (*1672* MU; *1706* OS).

Geum canadense Jacq.—Rare and local in SZ (*3038* OS).

G. laciniatum Murray—Occasional and scattered in PM, SZ, and WP (*3037* MU).

Rubus occidentalis L.—Occasional and scattered in SZ (*4771* MU).

Agrimonia parviflora Aiton—Occasional and scattered in PM and SZ (*3176* MU).

Rosa palustris Marshall—Abundant and scattered in SZ (*4783* MU).

Amelanchier spicata (Lam.) K. Koch.—Rare and local in SZ (*4534* OS).

LYTHRACEAE

Lythrum alatum Pursh—Occasional and scattered in MF (*3346* KE, OS).

Epilobium leptophyllum Raf.—Rare and local in PM (*3039* MU; *3160* OS).

E. coloratum Biehler—Occasional and scattered in GM, OW, and PM (*3189* OS).

Oenothera biennis L.—Rare and local in MF and WP (*2881* MU).

CORNACEAE

Cornus amomum Miller—Abundant and scattered in SZ (*3032* OS; *3662* MU).

Cornus sericea L.—Occasional and scattered in SZ (*2418* MU, OS).

AQUIFOLIACEAE

Ilex verticillata (L.) A. Gray—Occasional and local in SZ (*1685* OS; *3163* KE; *3652* MU).

RHAMNACEAE

[1]*Rhamnus frangula* L.—Occasional and scattered in PM and SZ (*4061* MU).

VITACEAE

Parthenocissus vitacea (Knerr) A. Hitchc.—Rare and local in PM (*4778* MU, OS).

Vitis riparia Michx.—Occasional and local in SZ (*3665* OS).

ANACARDIACEAE

Rhus glabra L.—Rare and local in WP (*4765* MU).

Toxicodendron vernix (L.) Kuntze—Occasional and scattered in PM and SZ (*1703* OS).

OXALIDACEAE

Oxalis stricta L.—Occasional and scattered in MF, PM, and WP (*3033* MU).

BALSAMINACEAE

Impatiens capensis Meerb.—Abundant and scattered in OW and SZ (*4066* MU; *4780* MU).

APIACEAE

Sanicula gregaria E. Bickn.—Rare and local in SZ (*3668* OS).

[1]*Daucus carota* L.—Occasional and scattered in WP (*3025* OS).

Cicuta bulbifera L.—Occasional and local in OW (*3168* OS).

GENTIANACEAE

Gentiana andrewsii Griseb.—Occasional and local in PM and SZ (*3175* MU; *3331* MU).

APOCYNACEAE

Apocynum cannabinum L.—Occasional and scattered in PM and WP (*3657* OS).

ASCLEPIADACEAE

Asclepias incarnata L.—Occasional and scattered in GM, PM, and OW (*3027* CLM).

SOLANACEAE

[1]*Solanum dulcamara* L.—Occasional and scattered in OW, PM, and SZ (*3653* OS).

CONVOLVULACEAE

[1]*Convolvulus arvensis* L.—Rare and local in WP (*3647* OS).

CUSCUTACEAE

Cuscuta gronovii Willd.—Occasional and scattered in OW, PM, and SZ (*1695* MU, OS).

BORAGINACEAE

[1]*Cynoglossum officinale* L.—Rare and local in WP (*3659* OS).

VERBENACEAE

Verbena hastata L.—Occasional and scattered in GM, OW, PM, and WP (*2722* OS; *3024* OS).

LAMIACEAE

Scutellaria lateriflora L.—Occasional and widespread in GM, OW, PM, SZ, and WP (*3185* MU).

S. galericulata L.—Occasional and scattered in GM, OW, and PM (*2618* CLM; *2725* MU).
S. nervosa Pursh—Occasional and local in OW and WP (*4781* MU).
Lycopus virginicus L.—Occasional and scattered in GM, OW, and PM (*3170* MU).
L. americanus Muhl.—Occasional and scattered in GM, OW, and PM (*3188* OS).
[1]*Nepeta cataria* L.—Rare and local in WP (*3914* KE).
Prunella vulgaris L.—Occasional and scattered in PM, SZ, and WP (*3030* OS).

OLEACEAE

Fraxinus pennsylvanica Marshall—Rare and local in SZ (*4770* MU).

SCROPHULARIACEAE

Mimulus ringens L.—Occasional and scattered in OW and PM (*2879* OS).
Agalinis purpurea (L.) Pennell—Occasional and scattered in GM, MF, OW, and PM (*1699* OS).

LENTIBULARIACEAE

[3]*Utricularia intermedia* Hayne—Rare and local in OW (*3334* KE).
U. vulgaris L.—Abundant and local in OW (*2621* CLM; MU).
U. gibba L.—Occasional and local in OW (*3042* OS).

CAMPANULACEAE

Campanula aparinoides Pursh—Abundant and scattered in GM and PM (*2723* MU; *4776* MU).
Lobelia kalmii L.—Occasional and widespread in GM and PM (*1700* OS).
L. siphilitica L.—Occasional and scattered in OW, PM, SZ, and WP (*3186* MU).

RUBIACEAE

Galium trifidum L.—Occasional and local in PM (*2885* OS; *3034* MU).

G. tinctorium L.—Occasional and scattered in GM, OW, PM, and SZ (*3918* CLM).
G. triflorum Michx.—Rare and local in SZ (*3921* KE).
G. aparine L.—Rare and local in SZ and WP (*3648* OS).

CAPRIFOLIACEAE

Viburnum lentago L.—Rare and local in SZ (*3664* OS).
Sambucus canadensis L.—Occasional and local in SZ (*3810* MU).

VALERIANACEAE

Valerianella umbilicata (Sulliv.) A. Wood—Rare and local in OW and WP (*2613* OS).

ASTERACEAE

Rudbeckia hirta L.—Occasional and local in WP (*3040* MU).
Bidens cernua L.—Occasional and scattered in MF, OW, PM, and WP (*1690* MU).
B. coronata (L.) Britton—Occasional and scattered in MF, OW, PM, and WP (*1675* MU; *1683* OS).
Ambrosia artemisiifolia L.—Rare and local in WP (*3159* MU).
[1]*Achillea millefolium* L.—Occasional and local in WP (*4774* MU).
[1]*Chrysanthemum leucanthemum* L.—Occasional and local in WP (*4777* MU).
Senecio aureus L.—Occasional and scattered in PM and WP (*4530* MU).
Erechtites hieracifolia (L.) Raf.—Rare and local in WP (*3333* OS).
Solidago patula Muhl.—Occasional and scattered in PM (*1707* MU).
S. rugosa Miller—Occasional and scattered in PM and WP (*1696* OS).
S. gigantea Aiton—Occasional and scattered in PM and WP (*3046* MU; *4069* KE).
S. canadensis L.—Occasional and local in WP (*4986* MU).
[4]*S. ohioensis* Riddel—Abundant and widespread in PM (*1677* MU).

S. riddellii Frank—Rare and local in PM (*1702* CLM).
Euthamia graminifolia (L.) Nutt.—Occasional and local in WP (*3158* MU).
Aster borealis Prov.—Rare and local in PM (*1705* OS).
A. puniceus L.—Abundant and widespread in GM, OW, PM, and WP (*1674* OS).
A. praealtus Poiret—Occasional and scattered in PM (*1681* OS).
A. lateriflorus (L.) Britton—Occasional and scattered in GM, PM, and WP (*1701* OS).
A. pilosus Willd.—Occasional and local in WP (*1687* OS).
A. novae-angliae L.—Rare and local in WP (*4985* MU).
A. umbellatus Miller—Abundant and widespread in GM and PM (*1704* OS).
Erigeron strigosus Muhl.—Rare and local in WP (*3036* OS).
Conyza canadensis (L.) Cronq.—Rare and local in WP (*3167* MU).
Eupatorium maculatum L.—Occasional and scattered in GM, OW, and PM (*1682* MU).
E. perfoliatum L.—Occasional and scattered in OW and PM (*3184* MU).
Cirsium muticum Michx.—Occasional and widespread in PM (*1697* OS).
[1]*C. vulgare* (Savi) Tenore—Occasional and scattered in WP (*3035* OS).
[1]*Taraxacum officinale* Weber—Rare and scattered in PM and WP (*4532* MU).
[1]*Cichorium intybus* L.—Occasional and local in WP (*4784* MU).

MONOCOTYLEDONS

ALISMATACEAE

Alisma subcordatum Raf.—Occasional and scattered in OW (*3023* CLM).
Sagittaria latifolia Willd.—Occasional and scattered in OW (*3026* MU).

POTAMOGETONACEAE

Potamogeton pectinatus L.—Abundant and widespread in OW (*4060* OS).
P. illinoensis Morong—Abundant and widespread in OW (*2728* OS, CLM; *2886* OS, CLM; *3049* OS).

NAJADACEAE

Najas flexilis (Willd.) Rostkov & Schmidt—Abundant and widespread in OW (*3992* MU).

LEMNACEAE

Lemna minor L.—Abundant and scattered in OW (*3336* OS).

COMMELINACEAE

[1]*Commelina communis* L.—Rare and local in WP (*3157* MU).

JUNCACEAE

Juncus canadensis J. Gay—Occasional and scattered in MF and PM (*1676* OS; *3172* MU).

J. brachycephalus (Engelm.) Buchenau—Occasional and scattered in MF (*1679* OS; *1686* MU).

J. torreyi Cov.—Occasional and scattered in GM, MF, and PM (*3057* CLM).

J. nodosus L.—Occasional and local in MF (*4782* MU).

J. articulatus L.—Occasional and scattered in MF (*3056* CLM; *4988* OS).

J. tenuis Willd. var. *dudleyi* (Wieg.) F.J. Herm.—Occasional and widespread in GM, MF, OW, PM, and WP (*3192* MU; *3660* MU).

CYPERACEAE

[2]*Scirpus smithii* A. Gray—Abundant and scattered in MF (*91671* OS; *1698* MICH; *3161* MU; *3345* KE).

S. acutus Muhl.—Occasional and local in OW (*3045* OS; *4779* MU).

S. validus Vahl.—Occasional and local in OW (*3183* OS).

S. fluviatilis (Torr.) A. Gray—Rare and local in GM (*4767* MU).

S. atrovirens Willd.—Occasional and scattered in OW (*2727* MU; *3055* OS).

S. pendulus Muhl.—Rare and local in GM (*4769* MU).

S. cyperinus (L.) Kunth.—Occasional and local in OW (*3171* MU).

[4]*Eriophorum viridicarinatum* (Engelm.) Fern.—Rare and local in PM (*2612* CLM, OS).

Eleocharis tenuis (Willd.) Schultes var. *borealis* (Svenson) Glea-

son—Occasional and scattered in GM and MF (*2623* CLM, OS; *3058* OS; *4070* MICH).

E. palustris L.—Occasional and scattered in OW (*3332* MU).

[3]*E. flavescens* (Poiret) Urban var. *olivacea* (Torr.) Gleason—Abundant and local in MF (*3166* OS; *3348* KE).

Fimbristylis autumnalis (L.) Roemer & Shultes—Abundant and scattered in MF (*1688* OS; *1693* MU; *3044* CLM).

[4]*Rhynchospora alba* (L.) Vahl.—Occasional and local in MF (*2882* MU, OS).

R. capillacea Torr.—Abundant and scattered in MF (*1691* MU).

[4]*Cladium mariscoides* (Muhl.) Torr.—Occasional and local in PM (*2884* OS).

Cyperus strigosus L.—Occasional and scattered in OW (*3051* CLM).

C. odoratus L.—Occasional and scattered in MF (*4073* MU).

C. flavescens L.—Occasional and local in MF (*4073* MU).

C. bipartitus Torr.—Occasional and local in MF (*1678* OS).

Dulichium arundinaceum (L.) Britton—Occasional and local in OW (*2878* MU).

[4]*Scleria verticillata* Muhl.—Occasional and scattered in MF and PM (*3041* OS).

Carex leptalea Wahlenb.—Abundant and scattered in GM and PM (*2419* CLM, OS).

[3]*C. sartwellii* Dewey—Rare and local in PM (*9001* OS).

C. vulpinoidea Michx.—Occasional and scattered in OW and WP (*2427* MU, OS; *2622* OS).

C. stipata Muhl.—Occasional and scattered in OW and WP (*2425* MU).

[4]*C. diandra* Schranck.—Rare and local in PM (*3658* OS).

C. interior L. Bailey—Occasional and scattered in GM and PM (*2430* MICH; *2431* OS).

[3]*C. bebbii* (L.H. Bailey) Fern.—Rare and local in PM (*2627* MICH; *3672* OS).

[4]*C. suberecta* (Olney) Britton—Rare and scattered in GM and PM (*2421* MICH, MU; *2628* MICH).

[4]*C. alata* T. & G.—Rare and local in PM (*2629* MICH; *3673* OS).

C. tetanica Schk.—Occasional and scattered in GM and PM (*2426* OS).

C. granularis Muhl.—Occasional and scattered in OW and WP (*2424* MU).

[4]*C. flava* L.—Occasional and widespread in GM and PM (*2423* CLM, MU, OS).

C. crinita Lam.—Occasional and scattered in OW and WP (*3350* MU).
C. comosa F. Boott—Occasional and scattered in OW and WP (*2625* OS; *3663* MU).
C. lacustris Willd.—Occasional and scattered in OW (*2429* OS).
[4]*C. utriculata* F. Boott—Occasional and scattered in OW (*2626* OS; *3667* MU).
C. lurida Wahlenb.—Occasional and scattered in OW and WP (*2428* MU, OS; *3919* KE).

POACEAE

Leersia oryzoides (L.) Swartz—Occasional and scattered in OW and WP (*3178* OS).
Festuca subverticillata (Pers.) E. Alexeev.—Rare and local on hummocks in SZ (*3670* OS).
[3]*Sphenopholis obtusata* (Michx.) Scribn. var. *obtusata*—Rare and local in PM (*3669* MU).
Phalaris arundinacea L.—Abundant and local in WP (*2721* OS; *4775* MU).
[4]*Calamagrostis stricta* (Timm) Koeler—Abundant and local in GM (*3920* MU).
Agrostis hyemalis (Walter) BSP. var. *scabra* (Willd.) Blomq.—Occasional and scattered in MF, PM, and WP (*4072* OS).
[1]*Phleum pratense* L.—Rare and local in PM (*4772* MU).
Muhlenbergia mexicana (L.) Trin.—Occasional and scattered in PM (*3177* OS).
M. glomerata (Willd.) Trin.—Occasional and scattered in PM (*4068* MU).
Panicum dichotomiflorum Michx.—Occasional and scattered in WP (*4071* MU).
P. flexile (Gattinger) Scribn.—Occasional and scattered in MF, PM, and WP (*3054* OS).
P. lanuginosum Elliott var. *implicatum* (Scribn.) Fern.—Occasional and scattered in PM and WP (*3053* OS).
Echinochloa muricata (P. Beauv.) Fern.—Occasional and scattered in OW and WP (*3187* MU; *4987* OS).

TYPHACEAE

Typha latifolia L.—Abundant and scattered in OW and WP (*3059* MU).
[1]*T. angustifolia* L.—Occasional and scattered in WP (*4773* MU).

IRIDACEAE

Iris virginica L.—Occasional and scattered in OW and PM (*2416* MU, OS).

ORCHIDACEAE

Spiranthes cernua (L.) Rich.—Occasional and local in MF (*3167* CLM, OS).

Habenaria lacera (Michx.) Lodd.—Rare and local in SZ (*2720* OS).

[3]*Pogonia ophioglossoides* (L.) Ker Gawler—Occasional and local in PM (*2609* CLM, OS).

[4]*Calopogon tuberosus* (L.) BSP.—Rare and local in PM (*2719* OS).

Liparis loeselii (L.) Rich.—Rare and local in SZ (*2610* CLM).

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OHIO DEPARTMENT OF NATURAL RESOURCES
DIVISION OF NATURAL AREAS AND PRESERVES
1889 FOUNTAIN SQUARE, BUILDING F
COLUMBUS, OHIO 43224

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GENETIC VARIATION IN MASSACHUSETTS POPULATIONS OF *CYPRIPEDIUM ARIETINUM* R. BROWN IN AIT. AND *C. ACAULE* AIT. (ORCHIDACEAE)

ALAN H. BORNBUSCH, LESLEY A. SWENDER, AND DEBORAH L. HOOGERWERF

ABSTRACT

Horizontal starch gel electrophoresis of isozymes was conducted on samples from the single currently known Massachusetts population of *Cypripedium arietinum* (ram's head lady's slipper) and two populations of *C. acaule* (pink lady's slipper). No genetic variation was detected at 27 presumptive loci in the *C. arietinum* population and only slight variation among 26 and 19 presumptive loci, respectively, in the *C. acaule* populations. Levels of polymorphism and heterozygosity in all populations were exceedingly low for animal pollinated obligate outcrossers. Genetic distance between the *C. acaule* populations was also low. Yearly and possibly overall effective population sizes in *C. acaule* and *C. arietinum* may be low due to low flower production and/or fruiting rate. Low levels of intrapopulation variation may thus result from genetic drift and founder effect, as proposed for *C. acaule* by Gill (1989). Low variation between *C. acaule* populations, though, indicates that genetic bottlenecks in ancestral populations may also have contributed to low species-level variation, as proposed by Case (1994) for Michigan populations of *C. acaule, C. arietinum, C. candidum,* and *C. reginae.* These results suggest that low genetic variation in declining *Cypripedium* populations may not be anthropogenic. These populations may have been genetically depauperate throughout much of their existence prior to human disturbance. Habitat loss, plant collecting and demographic stochasticities are, at least in the short term, more significant threats to *Cypripedium* populations than is a relative lack of genetic variation.

Key Words: *Cypripedium arietinum, Cypripedium acaule,* lady's slipper orchids, genetic variation, conservation

INTRODUCTION

How much variation exists in natural populations and what factors contribute to lower than expected intraspecific variation are questions of longstanding interest to evolutionary geneticists. These questions have also more recently assumed significance for conservation biologists. Low levels of variation in populations experiencing anthropogenic declines can represent "genetic deterioration" from higher levels that existed prior to disturbance (Simberloff, 1986). Low variation, though, can result from factors unrelated to modern anthropogenic disturbances. In plants, these factors include bottlenecks in ancestral populations due to climate

induced range contractions, adaptation to specialized and stable environments, evolution of primarily selfing mating systems with selection against homoygotes for certain alleles, and reproductive strategies that lower effective population sizes (Barrett and Kohn, 1991; Karron, 1991). Assessing the relative contributions of anthropogenic and natural factors to lowered genetic variation in a rare species can help define proximate threats to the species' survival and thus guide formulation of appropriate conservation strategies.

The genus *Cypripedium* (lady's slipper orchids) in North America includes 12 species (Luer, 1975; Wiard, 1987). Some species (e.g., *C. arietinum* R. Brown in Ait., *C. candidum* Muhl. ex Willd., *C. reginae* Walter) are experiencing rangewide declines and are listed by states as endangered, threatened or of special concern. Recent studies, based on Virginia or Michigan populations, have proposed that *C. acaule* Ait., *C. arietinum, C. candidum,* and *C. reginae* are depauperate in genetic variation due to life history characteristics and/or ancestral bottlenecks (Case, 1994; Gill, 1989). Here, we expand the database for assessing these hypotheses by documenting low levels of variation in Massachusetts populations of *C. acaule* and *C. arietinum.*

Lady's slipper orchids are noted for elaborate flowers that attract pollinators that enter the pouch-like labellum and can escape only by a pathway that facilitates cross-pollination. With only two known exceptions (*Cypripedium dickinsonianum* Hagsater, *C. passerinum* Richardson in Franklin), the complex floral structures also prevent self-pollination in the absence of pollinators (Catling, 1990; Stoutamire, 1967). Thus, although the flowers appear to offer no nectar reward or other food to pollinators, most *Cypripedium* species are obligate outcrossers dependent on insect pollination for sexual reproduction (van der Pijl and Dodson, 1966; Stoutamire, 1967).

Gill (1989) suggested that a dependence on insect pollination in combination with attraction by deceit has significant demographic consequences for populations of *Cypripedium acaule.* In a 10-year field study of a Virginia *C. acaule* population, Gill (1989) found the highest percentage of fruits produced by flowering plants in a given year was 7.1%. Six out of ten years, fruiting rates were below 1%, and in four of those years, no fruits were produced in a population with a geometric mean of 680.6 plants. Gill (1989) attributed these low fruiting rates to the failure of non-rewarding

flowers to attract pollinators repeatedly. Low rates of fruiting in *Cypripedium* have been observed in other populations, including *C. acaule* in Massachusetts, New Hampshire and New Brunswick (Barrett and Helenurm, 1987; Brackley, 1985; Davis, 1986; Plowright et al., 1980), *C. arietinum* in Wisconsin (J. Bender, pers. comm., 1992) and *C. candidum* in Ontario (Catling and Knerer, 1980; Falb and Leopold, 1993). Moreover, some of these studies and our observations indicate that annual flower production is also low in some *Cypripedium* populations. Populations of some *Cypripedium* species may thus have low effective population sizes (N_e, Hartl and Clark, 1989) in a single year due to low flower production and/or fruiting rates (Gill, 1989; Kimura and Crow, 1963). Furthermore, because establishment of a *C. acaule* population requires a multiplicative series of improbable events (e.g., seed dispersal and germination, seedling survival to reproductive maturity, and cross-pollination between founders), Gill (1989) suggests that *C. acaule* populations are subject to pronounced founder effects. Because the severities of genetic drift and founder effect are inversely proportional to N_e, these factors can lower genetic variation within populations with low N_e's (Hartl and Clark, 1989). It has thus been hypothesized by Gill (1989) that *C. acaule* populations should be particularly low in genetic variation because of reproductive patterns that substantially reduce N_e's. We note here, though, and discuss more fully below, that calculating overall N_e for a *Cypripedium* population is problematic. Overall N_e may be higher than indicated by annually low N_e's.

Although genetic drift can reduce intrapopulation variation, it can increase genetic variance among isolated populations, especially among populations that are founded by few individuals (Hartl and Clark, 1989). Because drift would act independently among isolated *Cypripedium acaule* populations, variation that is partitioned among these populations is thus expected to be significant. Case (1994), though, documented low variation within and between Michigan *C. acaule* populations. Similar patterns were observed in *C. arietinum, C. candidum* and *C. reginae* from the same region. Case (1994) thus proposed that ancestral populations of these species experienced genetic bottlenecks due to habitat loss and fragmentation during Pleistocene glaciations. Furthermore, extant conspecific populations in the Great Lakes region may have been derived by recolonization of glaciated areas

from a single genetically depauperate source population. Populations so derived would be low in variation and genetically similar to each other (Case, 1994).

This study is a genetic analysis of three *Cypripedium* populations: the only currently known Massachusetts population of *C. arietinum* (ram's head lady's slipper), and two of *C. acaule* (pink lady's slipper). Although *C. arietinum* has been described as locally abundant at some sites, it has historically been rare throughout its range, and anthropogenic habitat loss, collecting and biotic succession within habitats are possible causes of recent rangewide declines (Case, 1964; Luer, 1975; The Nature Conservancy, 1990). Several states officially list *C. arietinum* as endangered (e.g., Massachusetts, Minnesota), threatened (e.g., Maine, New York) or of special concern (e.g., Michigan) (Beaman et al., 1985; Coffin and Pfannmuller, 1988; Dibble et al., 1989; Sorrie, 1989; Young, 1992). *Cypripedium acaule,* by contrast, is common throughout its range, and is one of the most common orchids in North America (Luer, 1975).

The objectives of this study were to: (1) measure and compare genetic variation in the three *Cypripedium* populations using horizontal starch gel electrophoresis of isozymes; and (2) determine whether patterns of genetic variation observed by Case (1994) for some *Cypripedium* species in the Great Lakes region extend to these New England populations.

METHODS

The *Cypripedium arietinum* population is located in the vicinity of Mount Toby, Sunderland, Franklin County, MA. Although the history of this population is uncertain, *C. arietinum* has been noted from the Mt. Toby area since at least the nineteenth century (Tuckerman and Frost, 1875). Stone (1913, p. 9) described the species as "often found . . . quite plentifully" at a Mt. Toby site. The present *C. arietinum* population occurs at a site that is seasonally moist and includes eastern hemlock (*Tsuga canadensis*), and, as less abundant species, witch hazel (*Hamamelis virginiana*), red maple (*Acer rubrum*), gray and black birches (*Betula populifolia, B. lenta*), shagbark hickory (*Carya ovata*), American basswood (*Tilia americana*), and chestnut oak (*Quercus prinus*). A 1992 census identified 111 above-ground plants (ramets) (4 flowering) in the *C. arietinum* population (P. Martin-Brown, pers.

comm., 1993). Fifty-seven plants, including all flowering plants and plants representing the size range in the population, were sampled by removal of several cm^2 of leaf from each plant.

Two *Cypripedium acaule* populations were sampled: one in Northampton, Hampshire County, MA and another near the *C. arietinum* population. The Northampton site includes as the most abundant woody species mountain laurel (*Kalmia latifolia*), eastern white pine (*Pinus strobus*), white (*B. papyrifera*) and gray birches, witch hazel, and red and sugar (*A. saccharum*) maples; other abundant species include *Lycopodium* sp. and hay-scented (*Dennstaedtia punctilobula*) and Christmas (*Polystichum acrostichoides*) ferns. The Northampton site has experienced small-scale brush dumping which does not appear to have significantly affected the *C. acaule* population. We estimated the size of this population in 1992 as at least 250–300 above-ground plants (ramets). The Northampton population was sampled as follows. From the approximate center of the population eight 50 m transects were run. The transects were oriented according to randomly chosen compass headings; two headings were chosen in each of the four 90° quadrants (i.e., 0–89°, 90–179°, etc.). At every five meters along each transect, the nearest *C. acaule* plant not more than 2.5 m from the transect was sampled. Thirty-four plants were thus sampled. Additional plants were sampled within areas of high plant density.

All observed individuals (40), including flowering and non-flowering plants, were sampled from the Mt. Toby *Cypripedium acaule* population. This population, like the nearby *C. arietinum* population, occurs at a site dominated by eastern hemlock and, as less abundant species, gray birch and witch hazel.

Cypripedium acaule plants were sampled by removal of leaf tissue as for *C. arietinum*. All samples from the three populations were immediately placed on ice in the field and later stored at −80°C no longer than six months prior to preparation for electrophoresis.

Samples were ground in one of three grinding buffers (1 mg tissue per 0.005 ml buffer; Table 1). Grinding buffers were prepared according to Soltis et al. (1983) with the exception that 2-mercaptoethanol was added during grinding. Wicks dipped in ground tissue were used immediately for electrophoresis or stored at −80°C for up to nine days prior to use. Storage of wicks had no detectable effect on electrophoretic resolution.

Table 1. Enzymes assayed from sampled *Cypripedium arietinum* and *C. acaule* populations, and combinations of grinding and gel/electrode buffers used in electrophoresis. Enzyme abbreviations (EC numbers in parentheses): acid phosphatase, APH (3.1.3.2); aconitase, ACN (4.2.1.3); aldolase, ALD (4.1.2.13); aspartate aminotransferase, AAT (2.6.1.1); esterase, EST (3.1.1.–); fructose-1,6-diphosphatase, F-1,6-PD (3.1.3.11); glutamic dehydrogenase, GDH (1.4.1.2); isocitrate dehydrogenase, IDH (1.1.1.42); leucine aminopeptidase, LAP (3.4.11.–); malate dehydrogenase, MDH (1.1.1.37); malic enzyme, ME (1.1.1.40); peroxidase, PER (1.11.1.7); phosphoglucoisomerase, PGI (5.3.1.9); phosphoglucomutase, PGM (5.4.2.2); 6-phosphoglucose dehydrogenase, 6-PGD (1.1.1.44); shikimate dehydrogenase, SKDH (1.1.1.25); triosephosphate isomerase, TPI (5.3.1.1). Grinding buffers named and gel/electrode buffer systems numbered as in Soltis et al. (1983).

	Grinding Buffer		Gel/Electrode Buffer	
Enzyme	*C. arietinum*	*C. acaule*	*C. arietinum*	*C. acaule*
APH	phosphate	tris-HCl	2	2
ACN	—	tris-HC1	—	8
ALD	—	phosphate	—	11
AAT	tris-HCl	tris-HC1	8	8
EST	phosphate	tris-HCl	7	7
F-1,6-PD	—	phosphate	—	11
GDH	phosphate	phosphate	7	7
IDH	tris-maleate	tris-HCl	2	2
LAP	phosphate	tris-HCl	2	5
MDH	tris-HCl	tris-HCl	5	5
ME	tris-maleate	tris-maleate	7	5
PER	tris-maleate	tris-maleate	2	8
PGI	phosphate	tris-HCl	2	2
PGM	phosphate	phosphate	2	2
6-PGD	tris-HCl	tris-maleate	5	5
SKDH	phosphate	phosphate	2	2
TPI	phosphate	phosphate	2	2

Methods of gel preparation, loading and slicing followed in general those outlined by Murphy et al. (1990). Details of our methods can be provided by the senior author upon request. Buffer systems were discontinuous and gel and electrode buffers were prepared according to Soltis et al. (1983). Combinations of grinding, gel and electrode buffers that provided satisfactory electrophoretic resolution were established for 17 enzyme systems (Table 1). Enzyme stains were prepared according to Soltis et al. (1983); leucine aminopeptidase (LAP) was stained according to

Wendel and Weeden (1989). Following staining, all gel slices were fixed in 50% glycerol or ethanol and stored at 2°C for future reference. Interpretations of observed banding patterns were based on reviews of quaternary structures and isozyme numbers by Gottlieb (1981) and Weeden and Wendel (1989). Isozymes were numbered and alleles at a locus lettered sequentially cathodal to anodal. Interpopulation comparisons for *C. acaule* were facilitated by co-electrophoresis with the same individual (from the Northampton population) as a standard for both populations.

RESULTS

For *C. arietinum,* satisfactory electrophoretic resolution was obtained for 27 presumptive loci (14 enzyme systems). The average sample size per locus was 36.0 individuals (Table 2). No variation was detected at any locus in our sample (Figure 1).

For the Northampton *C. acaule* population, satisfactory electrophoretic resolution was obtained for 26 presumptive loci (16 enzyme systems). The average sample size per locus was 36.7 individuals (Table 2). Allelic variation was observed at four loci (allele frequencies in parentheses): LAP (a—0.04, b—0.96); PER-2 (a—0.22, b—0.78); PGI-1 (a—0.08, b—0.92, Fig. 2a); PGM (a—0.01, b—0.99, Fig. 2b). The proportion of polymorphic loci was 15.4%; polymorphism by 95% criterion, 7.7% (Ayala, 1982); average number of alleles per locus (standard error in parentheses), 1.15 (0.072); average effective number of alleles per locus, 1.03 (0.021) (Hartl and Clark, 1989); and unbiased estimate of average heterozygosity per locus, 0.023 (0.015) (Nei, 1978).

For the Mount Toby *C. acaule* population, satisfactory electrophoretic resolution was obtained for 19 presumptive loci (15 enzyme systems). The average sample size per locus was 27.9 individuals (Table 2). Allelic variation was identified at one locus (allele frequencies in parentheses): PGI-2 (a—0.015, b—0.985). The proportion of polymorphic loci was 5.3%; polymorphism by 95% criterion, 0%; average number of alleles per locus (standard error in parentheses), 1.05 (0.053); average effective number of alleles per locus, 1.00 (0.002); and unbiased estimate of average heterozygosity per locus, 0.0016 (0.0016).

The two *C. acaule* populations were isomorphic at all loci that were invariant in both populations and no locus was polymorphic in both populations. At a locus that was polymorphic in one

Table 2. Sample sizes (*n*) for loci scored from sampled populations of *Cypripedium arietinum* and *C. acaule*.

C. arietinum		*C. acaule*		
Locus	*n*	Locus	*n* (Northampton)	*n* (Mount Toby)
AAT	38	AAT-1	36	40
APH-1	40	AAT-2	36	20
APH-2	40	ACN	33	—
APH-3	40	ALD-1	35	—
APH-4	40	ALD-2	32	—
EST-1	40	APH	42	34
EST-2	40	EST-1	42	36
EST-3	39	EST-2	42	35
EST-4	39	F-1, 6-PD	—	26
EST-5	36	GDH	36	26
GDH	36	IDH-1	41	21
IDH	39	IDH-2	35	—
LAP-1	27	LAP	37	22
LAP-2	30	MDH-1	42	37
MDH-1	29	MDH-2	38	—
MDH-2	30	MDH-3	38	—
MDH-3	33	MDH-4	42	—
ME	40	ME	42	40
PER-1	21	PER-1	35	10
PER-2	39	PER-2	30	11
PGI-1	40	PGI-1	39	33
PGI-2	40	PGI-2	42	33
PGM	35	PGM	38	13
6-PGD	23	6-PGD	42	40
SKDH-1	40	SKDH	21	24
SKDH-2	40	TPI-1	32	29
TPI	39	TPI-2	27	—

population, the most common allele was fixed in the other population. Genetic distance between the two *C. acaule* populations, estimated at 18 loci according to Nei (1978), was thus low, 0.0028.

DISCUSSION

The levels of genetic variation measured from the three sampled *Cypripedium* populations are among the lowest measured for plants by isozyme methods, and are anomalous for animal pollinated outcrossers. Hamrick and Godt (1990), for example, found that

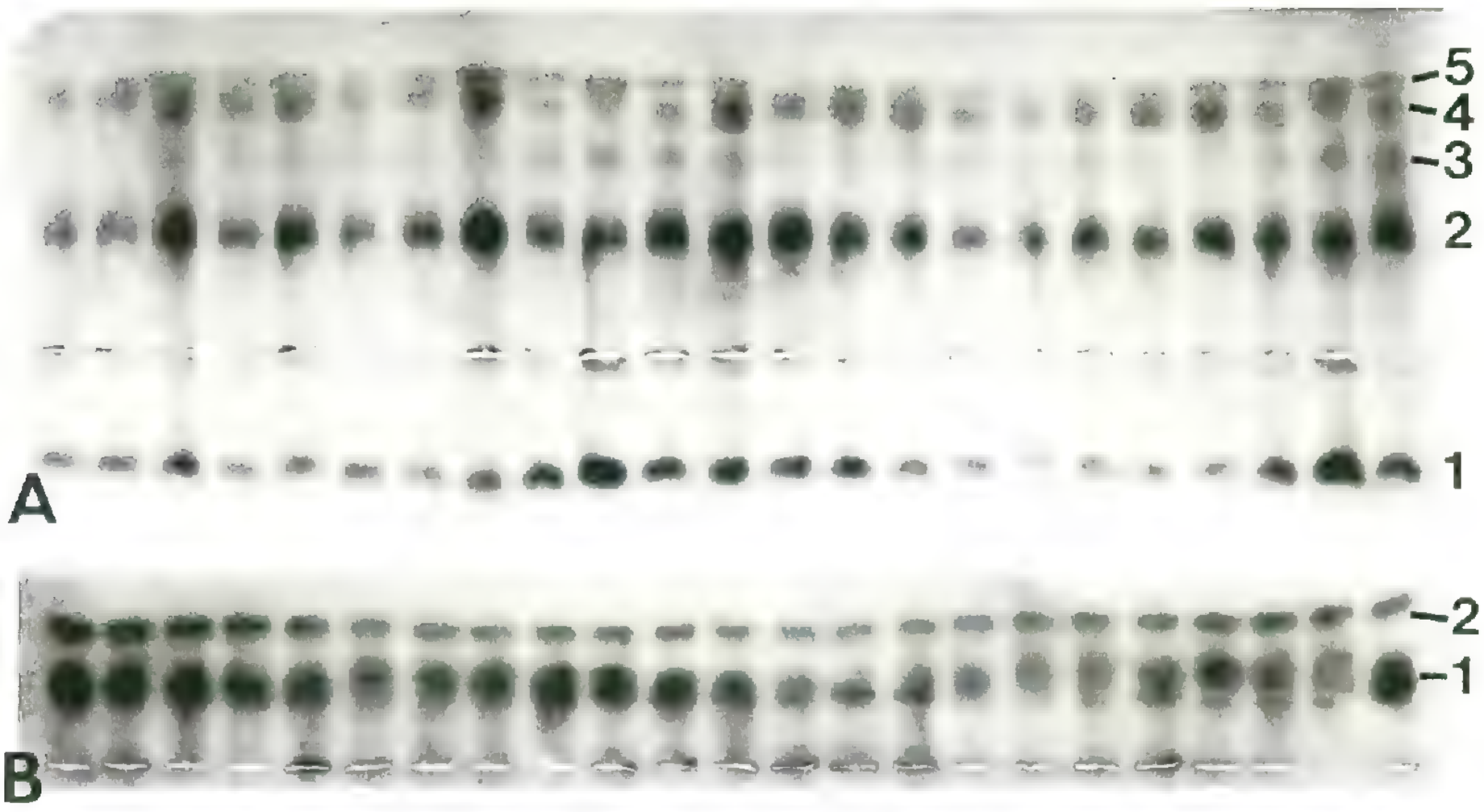

Figure 1. Electrophoretic patterns observed in *Cypripedium arietinum* population for: **A,** esterase; **B,** phosphoglucoisomerase. Isozymes numbered on right as in Table 2. Each gel shows eleven individuals, each loaded twice, and one control individual. Anode is toward the top on each gel.

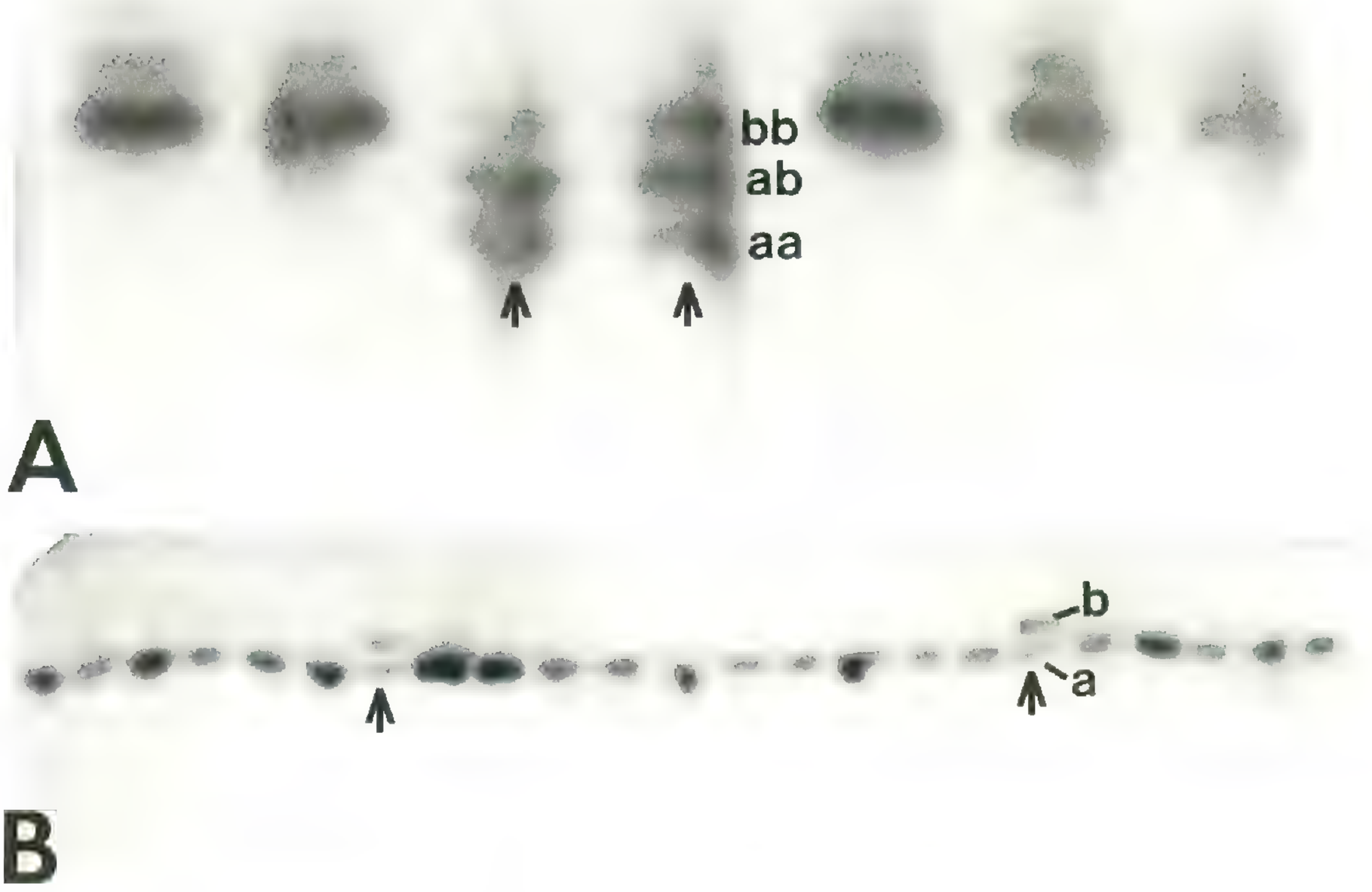

Figure 2. Electrophoretic patterns observed in Northampton *Cypripedium acaule* population for: **A,** phosphoglucoisomerase-1 (seven individuals shown; arrows indicate two heterozygotes with homodimeric (aa, bb) and heterodimeric (ab) bands); **B,** phosphoglucomutase (11 individuals, each loaded twice, and one control individual shown; arrows indicate heterozygote with two monomeric (a, b) bands). Anode is toward the top on each gel.

the average proportion of polymorphic loci among populations of 80 monocots was 40.3% (standard error 3.0). Obligate outcrossing is often associated with high levels of genetic variability, and Hamrick and Godt (1990) found the average proportion of polymorphic loci in animal pollinated outcrossers was 35.9% (1.8) (see also Hamrick et al., 1991).

Loci examined in our study included some of the most variable isozyme loci assayed in plants (e.g., esterases, phosphatases and peroxidases; Gottlieb, 1981). Additionally, although our population sample sizes were not unusually large, 19–27 presumptive loci were assayed in each population and increasing the number of assayed loci is considered more important that enlarging sample size when estimating genetic variation (Gorman and Renzi, 1979; Nei, 1978). Interpreting the number of loci (isozymes) for an enzyme system with monomorphic banding can be difficult and for some systems we may have overestimated by a few loci the number of actual observed loci. This, however, would not affect our overall finding of low genetic variation. Hence, although our results are striking, we do not believe that they are artifacts of locus choice or number.

Our findings are in agreement with those of Case (1994) who found a complete lack of variation at 11 loci in four *Cypripedium arietinum* populations and low variation in four *C. acaule* populations in Michigan. Reduced levels of polymorphic loci and/or heterozygosity were also identified in Michigan populations of *C. candidum* and *C. reginae,* but *C. calceolus,* by comparison, had unusually high levels of variation (Case, 1993, 1994). Klier et al. (1991) reported similar findings for Iowa populations of *C. candidum* and *C. calceolus.*

Based on the demographics of *Cypripedium acaule* populations, Gill (1989) speculated that repeated genetic bottlenecks and founder effect, resulting from reproductive patterns that lower N_e's, may lower intrapopulation variation in *C. acaule.* According to Gill (1989), a *C. acaule* population may begin as a sample of a source population, but, because of infrequent cross-pollination, only a few of the founders contribute to future cohorts. Founder effect may leave these cohorts with little variation and subsequent inbreeding among closely related progeny may further reduce population heterozygosity.

In an established *Cypripedium* population, population-level changes in allele frequencies due to genetic drift are a function of

the population's overall N_e. The N_e of a *Cypripedium* population in a given year is determined in part by the number of plants that flower and are pollinated. The percentage of plants which have flowered in the Massachusetts *C. arietinum* population has ranged from 3.6% to 25.3% during the period 1985–1992, with a harmonic mean of 11.7 plants. The geometric mean of the number of above-ground plants, by contrast, was 141.6 (P. Martin Brown, pers. comm., 1993). In the sampled Northampton *C. acaule* population, only five plants flowered among the 241 plants located in 1992. In the *C. acaule* population studied by Gill (1989), the geometric mean of above-ground plants over a ten-year period was 680.6, but the harmonic means of flowering and fruiting plants were only 33.0 and 3.2, respectively. As demonstrated by these examples, established *C. acaule* and *C. arietinum* populations may experience genetic bottlenecks between cohorts to an extent not indicated by measures of population size N.

Population-level changes in genetic variation due to drift, though, are more dependent on a population's overall N_e across cohorts. Although annual N_e's may be low in *Cypripedium acaule* and *C. arietinum* populations, overall N_e's may not be as low. Kimura and Crow (1963) estimate the overall N_e of a population as the harmonic mean of the N_e's for each generation (hence, our use of the harmonic mean above). However, for long-lived perennials that do not flower every year, like *Cypripedium,* this method may underestimate, if only slightly, overall N_e. Gill (1989) showed that *C. acaule* plants may enter a subterranean dormancy for one to five years and there is little pattern to which individuals appear above ground and flower or fruit in a given year. Thus, although in a single year few individuals reproduce, reproduction over several years in a *Cypripedium* population may be spread across a larger number of different individuals. If, for example, five individuals reproduce in one year and five different individuals reproduce the following year, the N_e for each year is five and the harmonic mean estimate of N_e across the two years is also five. (We assume for this argument that progeny are produced in equal proportions among all reproducers.) More than five individuals, though, have contributed in the two years to future cohorts. The overall N_e for the two years is thus greater than five, but less than ten since the first five individuals had no chance to mate with the second five. Our purpose in this argument is to suggest that population-level losses in genetic variation due to

drift in *C. acaule* and *C. arietinum* can be overestimated if annual N_e's are used as indicators of overall N_e's. The fact remains, though, that the numbers of reproducing (fruiting) individuals in a *C. acaule* or *C. arietinum* population are annual extremely low and, even if flowering were random among individuals, overall N_e would still be unusually low.

Although founder effect and genetic drift may thus contribute to low levels of intrapopulation variation in *Cypripedium acaule* and *C. arietinum,* these forces should also act to increase variance in allele frequencies between isolated populations. Our results and those of Case (1994), though, indicate low species-level diversity in *C. acaule* and *C. arietinum.* Furthermore, Case (1993, 1994) and Klier et al. (1991) showed that *C. calceolus,* although presumably similar to other *Cypripedium* species in life history characteristics, has unusually high levels of variation. Case (1994) thus proposed that ancestral genetic bottlenecks caused by glacial disturbance of habitats have contributed to lowered variation in the relatively ecologically and geographically restricted *C. acaule, C. arietinum, C. candidum,* and *C. reginae.* Case (1994), though, cautioned that her results were based on populations in the Great Lakes portion of *Cypripedium* ranges. Our study sampled New England populations and indicates that, at least for *C. acaule* and *C. arietinum,* the patterns of genetic variation documented by Case (1994) extend beyond the Great Lakes region.

In some respects, the Massachusetts *Cypripedium arietinum* population is a marginal population: it is at the margin of its species' range, and flower production, although variable in a ten-year period, has been low overall (Luer, 1975; see Soulé, 1973 and Grant and Antonovics, 1978 for criteria of marginality). It has been suggested that marginal populations may differ in genetic composition (e.g., be less variable) from more central ones due to greater drift, lowered immigration, or stronger and/or different selection pressures (Soulé, 1973). However, isozyme studies of plants have not revealed a consistent pattern in genetic variation between geographically marginal and central populations (e.g., Levin, 1977; Tigerstedt, 1973). Studies of phenotypic and genetic variation at ecologically marginal versus more central sites have also shown no consistent pattern (Agnew, 1968; Linhart, 1974). Furthermore, the low variation in the Northampton and Mount Toby *C. acaule* populations, which are neither geographically nor ecologically marginal for the species, indicates that it would be

premature to attribute the low variation in the Massachusetts *C. arietinum* population to its marginality.

An implication of our findings and those of Case (1994) is that low genetic variation in declining *Cypripedium* populations may not be the result of anthropogenic factors. These populations may not be experiencing "genetic deterioration" (*sensu* Simberloff, 1986) from previously high levels of variation. Rather, these populations may have been genetically depauperate throughout much of their existence prior to human disturbance due to a combination of historical events (Pleistocene bottlenecks) and reproductive patterns (low flower and/or fruit production) that lower effective population sizes. We suggest that habitat loss, plant collecting and demographic stochasticities are, at least in the short term, more significant threats to *Cypripedium* populations than is a relative lack of genetic variation. Strategies that combine habitat protection and management and enhancement of population size may be the most appropriate means of conserving these populations. Conservation strategies could include: (1) maintenance of suitable habitat by partial canopy opening to offset natural successional change (Falb and Leopold, 1993; Mitchell and Sheviak, 1981; The Nature Conservancy, 1990); (2) managing *Cypripedium* sites for a diversity of flowering plants that offer rewards to attract and retain pollinators at the sites (Catling and Knerer, 1980; Davis, 1986; Falb and Leopold, 1993); (3) and although labor intensive, hand pollination to increase fruit production (Davis, 1986; Gill, 1989; Barrett and Helenurm, 1987).

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DEPARTMENT OF BIOLOGICAL SCIENCES
SMITH COLLEGE
NORTHAMPTON, MASSACHUSETTS 01063

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EXINE REDUCTION IN UNDERWATER FLOWERING *CALLITRICHE* (CALLITRICHACEAE): IMPLICATIONS FOR THE EVOLUTION OF HYPOHYDROPHILY

C. Thomas Philbrick and Jeffrey M. Osborn

ABSTRACT

Both aerial and underwater pollination systems (hypohydrophily) occur in *Callitriche* (Callitrichaceae), and as such the genus can serve as a model system in which to probe questions concerning the evolution of hypohydrophily from aerial pollination systems. Evidence from scanning and transmission electron microscopy reveals strikingly different exine thickness in the pollen of four aerially flowering species (*C. heterophylla* var. *bolanderi*, *C. marginata*, *C. peploides*, and *C. stagnalis*), which have a distinct sexine layer (0.55–1.1 μm thick), in comparison with that of the hypohydrophilous *C. hermaphroditica*. The exine of the latter species is rudimentary (<0.1 μm thick) in pollen of the annual form of the species, and virtually absent in the perennial form. The degree of exine reduction in pollen of *C. hermaphroditica* relative to that of the aerially flowering species contrasts with the otherwise general morphological similarity observed among the flowers of the respective species.

Key Words: *Callitriche*, underwater pollination, pollen ultrastructure

INTRODUCTION

Although considerable insight has been gained regarding pollen form and function in angiosperms (e.g., Blackmore and Ferguson, 1986 and refs. therein) a general consensus remains elusive concerning possible relationships between pollen morphology and pollination systems. Several studies have shown positive correlations between pollen structure and the nature of the pollen vector (e.g., anemophilous compositae, Bolick, 1990; papilionoid legumes, Ferguson and Skvarla, 1982; Araceae, Grayum, 1986; Cambombaceae, Osborn, Taylor, and Schneider, 1991), whereas others report a lack of such associations (e.g., Polemoniaceae, Taylor and Levin, 1975; various families, Lee, 1978; Zingiberales, Kress, 1986). Factors that are indirectly related to pollination may also play a role in influencing the evolution of pollen structure, especially pollen–stigma interactions (see Kress, 1986).

In contrast, a striking correlation exists between pollen structure and pollination system in species that exhibit underwater cross-pollination systems (hypohydrophily). Reduction of exine thickness, or the lack of exine altogether, is strongly correlated with

hypohydrophily (Cox, 1988; Philbrick, 1988; Philbrick and Anderson, 1992). For instance, pollen of hypohydrophilous species from often distantly related groups have rudimentary exines, including *Ceratophyllum demersum* L. (Ceratophyllaceae: Les, 1988), *Enhalis acoroides* (L.) Royle and *Thalassia hemprichii* (Ehrenb.) Aschers. (Hydrocharitaceae: Pettitt, 1980, 1981), while an exine component of the pollen wall is absent in *Thalassodendron ciliatum* (Forsk.) den Hartog (Hydrocharitaceae; Pettitt, 1980), and species of *Najas* (Najadaceae: Blackmore, McConchie, and Knox, 1987) and *Amphibolis* (Cymodoceaceae: Pettitt, Ducker, and Knox, 1978). Indeed, exine reduction is one of the few morphological features that are unique to hypohydrophilous pollination systems.

Few comparative studies have been conducted at the infrageneric level between aerially flowering and hypohydrophilous species. Clearly the major hindrance to such comparisons is the fact that genera that have both pollination types are exceedingly rare. As a consequence, our understanding of the nature of the changes that take place in pollen structure, indeed in all floral structure, during the evolution of hypohydrophily are based on comparisons at the generic level and above. Yet, comparisons at these higher taxonomic/phylogenetic levels are of limited value for understanding features that are as evolutionarily dynamic as pollination systems. *Callitriche* is an ideal genus for such comparisons because both aerial and hypohydrophilous pollination systems occur.

Callitrichaceae is a widespread monogeneric (*Callitriche*) family of ca. 50 species. Species of *Callitriche* exhibit one of three growth habits: terrestrial, amphibious, or aquatic (Philbrick and Anderson, 1992 and refs. therein). Terrestrial species occur in seasonally wet areas while plants of amphibious species can grow submersed, with a floating rosette of leaves, or as the land-form on moist ground. Aquatic species grow obligately submersed.

Callitriche is the only genus in which both aerial floral biologies and hypohydrophily have been documented (Philbrick and Anderson, 1992; Philbrick, 1993). The majority of species of *Callitriche* flower aerially; anemophily seems to be the principal pollination system. *Callitriche truncata* Gussone and *C. hermaphroditica* L. show obligately submersed flowering. Philbrick (1993) has employed paternity exclusion analysis using random amplified polymorphic DNA markers to document hypohydrophily in *C. hermaphroditica*. The pollination system of *C. truncata* is poorly known.

The high degree of floral structural divergence between aerial flowering and hypohydrophilous angiosperms is well known (e.g., Arber, 1920; Dahlgren and Rasmussen, 1983; Philbrick, 1991; Sculthorpe, 1967; Tomlinson, 1982). A significant component of this divergence entails loss or reduction of parts (e.g., perianth, number of stamens) and reduction in flower size. Consequently, one would predict that a similar degree of divergence would occur between aerially flowering and hypohydrophilous species of *Callitriche*. However, this is not the case. The overall floral morphology of species of *Callitriche* is uniform (cf., Philbrick and Anderson, 1992; Schotsman, 1982, 1985). The only qualitative difference in reproductive structures of aerial and submerged flowering species is the presence (aerial flowering species) or absence (submerged flowering species) of endothecial thickenings in the anthers (Schotsman, 1982; Philbrick, unpubl.).

Although several studies of pollen morphology of *Callitriche* have been published based on data obtained using light and scanning electron microscopy (SEM) (e.g., Diez, Talavera, and Garcia-Murillo, 1988; Martinsson, 1993; Moar, 1960; Moore and Webb, 1978) the diversity of pollen ultrastructural features that occur in the genus are not well understood. Only two investigations have provided structural information on *Callitriche* pollen based on transmission electron microscopy (Martinnson, 1993; Osborn and Philbrick, 1994).

Herein we address the question, how does exine thickness in the hypohydrophilous *Callitriche hermaphroditica* compare with that of aerial flowering species? This question is addressed by comparative study of exine thickness of four aerially flowering species of *Callitriche* and the hypohydrophilous *C. hermaphroditica*.

MATERIALS AND METHODS

Species Studied

Five species were studied: *C. hermaphroditica* L., *C. heterophylla* var. *bolanderi* (Hegelm.) Fassett, *C. marginata* Torrey, *C. peploides* Nutt., *C. stagnalis* Scop. Voucher specimens are listed in Appendix I. Four of the five species studied (except *C. hermaphroditica*) are aerially pollinated, and are presumed to be anemophilous although little experimental evidence confirms this.

Callitriche hermaphroditica is hypohydrophilous (Philbrick, 1993). One species (*C. heterophylla* var. *bolanderi*) was also selected that exhibits internal geitonogamy, an unusual form of self-fertilization (Philbrick, 1984; Philbrick and Anderson, 1992).

The species selected represent all three growth habits that occur in the genus. *Callitriche heterophylla* var. *bolanderi, C. marginata,* and *C. stagnalis* are amphibious. *Callitriche peploides* is terrestrial and *C. hermaphroditica* is aquatic. Moreover, these species represent the three main phylogenetic lineages in the genus (Philbrick and Jansen, 1991).

Electron Microscopy

Entire plants were fixed in formalin : glacial acetic acid : 95% ethanol (FAA; 0.5:0.5:9). For SEM, pollen of all species except *C. hermaphroditica* was acetolyzed and prepared as outlined in Bogle and Philbrick (1980). Grains of *C. hermaphroditica,* which collapse even after mild acetolysis, were critical point dried, dehydrated in a graded ethanol series, and placed onto aluminum stubs. Grains were examined on scanning electron microscopes at the University of Connecticut and the Rancho Santa Ana Botanic Garden.

For transmission electron microscopy (TEM), mature anthers were excised from preserved plants, post-fixed in 1% osmium tetroxide, buffered in sodium cacodylate to a pH of 6.5, for 2 h and washed with buffer. Entire anthers were placed onto cellulose filters and then coated on both sides with agar. Agar embedded filters were subsequently dehydrated in a graded ethanol series, transferred to several changes of 100% acetone (to solubilize the filters), gradually infiltrated with Spurr low viscosity epoxy resin, and embedded. Ultrathin sections were cut with a diamond knife, collected on copper 1 × 2 mm slot grids, and dried onto formvar support films following the techniques of Rowley and Moran (1975). Grids were stained with 1% potassium permanganate (1–5 min.), 1% uranyl acetate (8–15 min.), and lead citrate (5–10 min.; Venable and Coggeshall, 1965), and examined using a Zeiss EM-10 transmission electron microscopy at 60–80 kV.

RESULTS

Both intine and exine sporoderm components of the grains were present, at least in part, in the pollen of all five species examined.

Not surprisingly, given that grains were fixed in F.A.A., the degree to which the intine was preserved in the various species differed. This limited interpretation regarding intine structure, but did not adversely affect interpretation of exine thickness, the main focus of the study. In general, the intine of *C. hermaphroditica* was well preserved while in the other four species it was not. The sporoderm fine structure of nonapertural wall regions, with particular emphasis on the layers, is presented below for each species.

C. heterophylla* var. *bolanderi

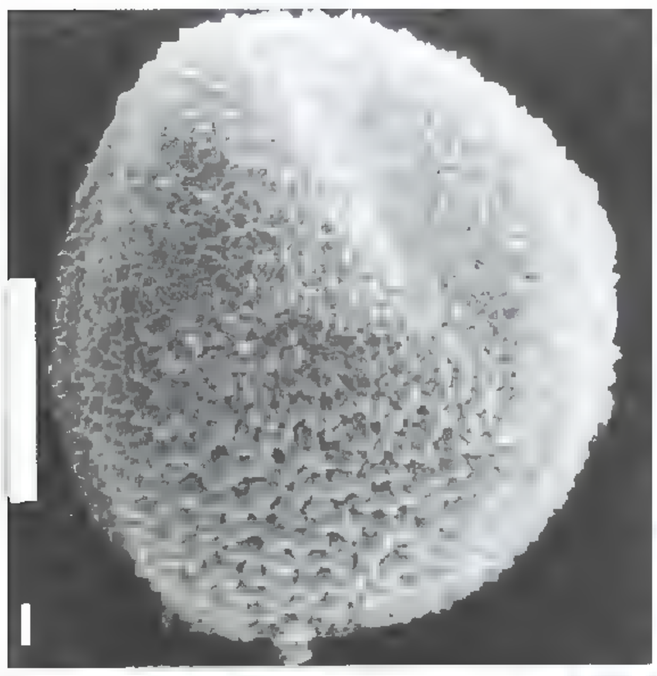
The grains of *Callitriche heterophylla* var. *bolanderi* (Figures 1–3) had a distinct exine component that ranged in thickness from 0.75–1.00 μm. The exine was intectate, and two-layered (sexine, nexine; cf. Erdtman, 1952), with the layers separated by a dark-staining commissural line (Figure 3). The sexine was composed of variably sized gemmae that formed an anastomosing to somewhat reticulate pattern (Figure 1). The gemmae were laterally fused at their bases, and in association with smaller granular elements formed a thin, somewhat irregular nexine (Figure 3). The nexine comprised about 20% of the total thickness of the overall exine. Below the commissure, relatively small granular elements of the nexine protruded into the underlying intine (Figure 3).

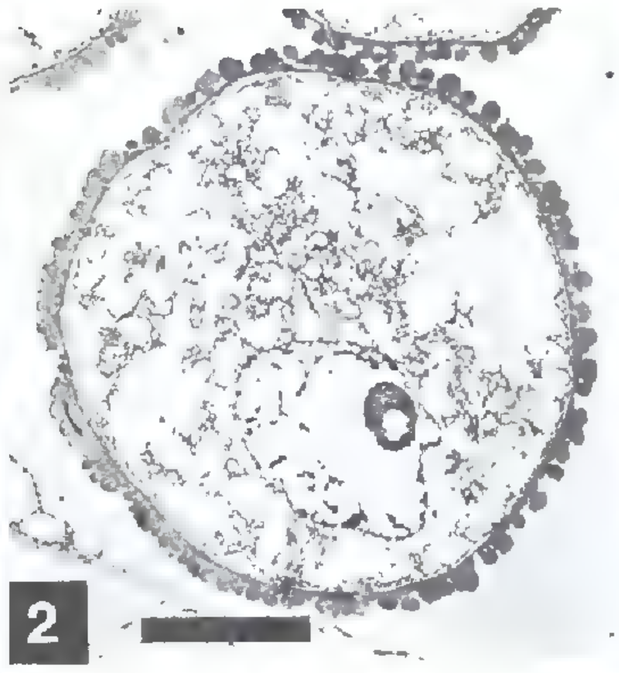
C. marginata

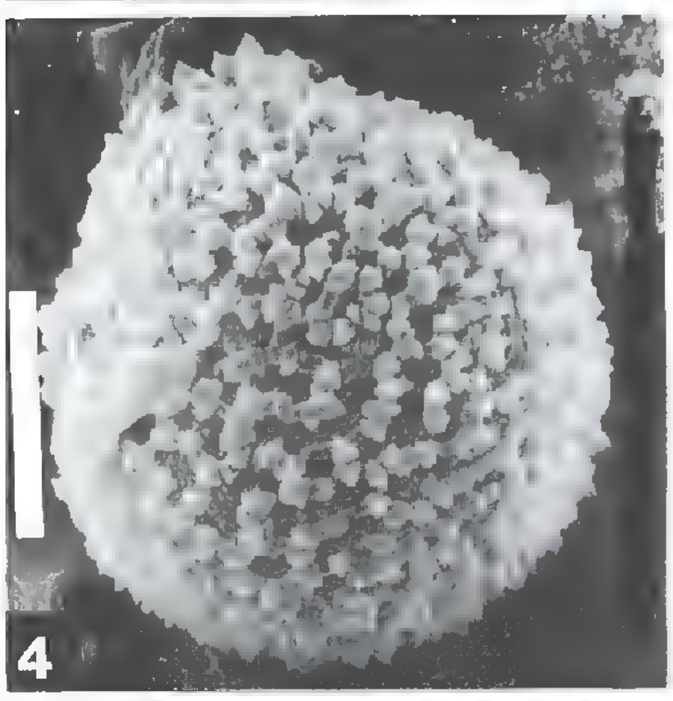
Pollen of *C. marginata* had a well-defined, two-layered, intectate exine that ranged from 0.55–1.17 μm in thickness (Figures 4–6). The sexine consisted of distinct elements ranging from gemmae to echinae that were fused laterally into a semi-reticulate pattern (Figure 4). A thin, somewhat continuous granular nexine was also present (Figure 6), and comprised approximately 10% of the total thickness of the exine. Larger granule units of the nexine were present below the more continuous layer, and penetrated into the underlying intine (Figure 6). A commissural line was indistinct.

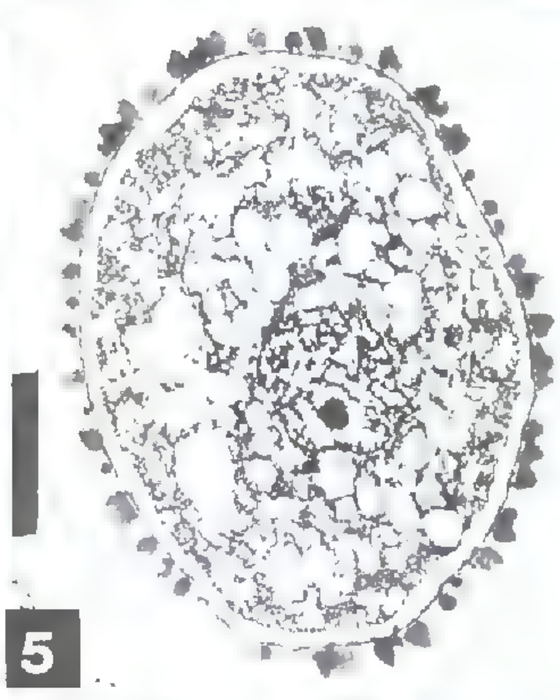
C. peploides

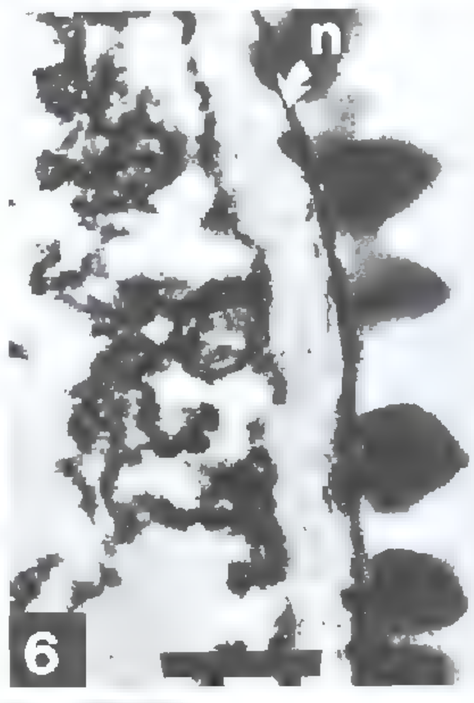
Pollen of *C. peploides* had a distinct, intectate exine that ranged from 0.70–0.95 μm thick (Figures 7–9). The exine of this species

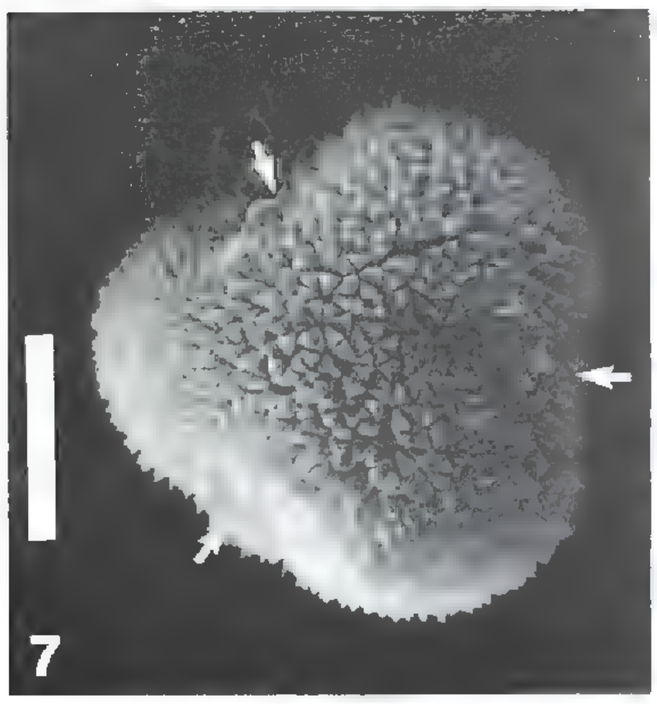


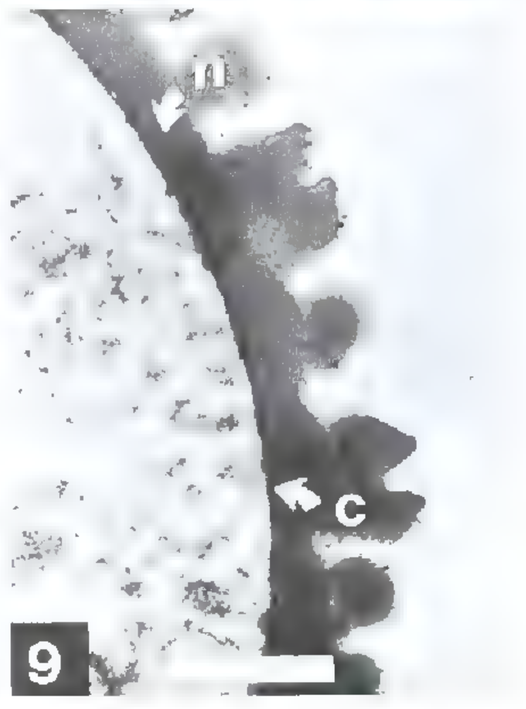












Figures 1–9. Scanning (Figures 1, 4, 7) and transmission (Figures 2, 3, 5, 6, 8, 9) electron micrographs of *Callitriche* pollen. Figures 1–3; *C. heterophylla* var. *bolanderi*. **1.** View showing interapertural region, aperture is evident as an elongate depression in the upper right region of the grain. Bar = 5 μm. **2.** Transverse section of entire grain. Bar = 5 μm. **3.** Detail of nonapertural exine in transverse section; note the nexine (n) and commissural line (c). Bar = 1 μm. Figures 4–6; *C. marginata*. **4.** View showing the interapertural region. Bar = 5 μm. **5.** Transverse section of entire grain. Bar = 5 μm. **6.** Detail of nonapertural exine in transverse section; note the nexine (n) relative to the thickness of the sculptured sexine. Bar = 1 μm. Figures 7–9; *C. peploides*. **7.** Polar view and the location of the three apertures (arrows); note the organization of the sculptural elements into polygonal shaped clusters. Bar = 5 μm. **8.** Transverse section of entire grain showing the location of apertures, denoted by the concave areas; note that apertural regions also have sculptured sexine elements, but a thinner nexine in comparison with nonapertural areas. Bar = 7 μm. **9.** Detail of nonapertural exine in transverse section; note the relative thickness of the nexine (n) versus the sculptured sexine, and the commissural line (c). Bar = 1 μm.

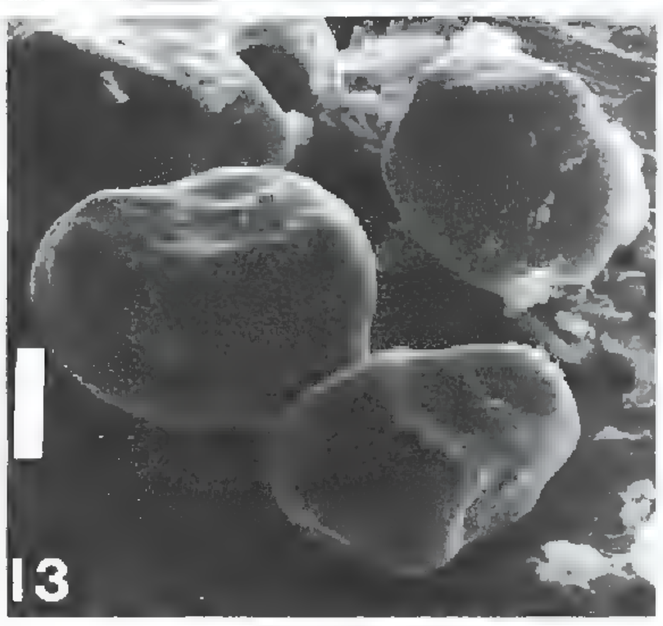
was also two-layered, with the sexine being composed of irregularly shaped verrucae and echinae. These outer sculptural elements were laterally fused at their bases and arranged in groups of 4–8 into polygonal shaped clusters (Figure 7). The sculptural elements were borne upon a relatively thick, homogeneous to granular nexine (Figure 9). The nexine of *C. peploides* was the thickest of the five species examined and accounted for about 30% of the total exine thickness. A dark commissure was present near the base of the nexine, and was in turn underlaid by a thin layer, that was somewhat irregular in thickness, consisting of minute granules (Figure 9).

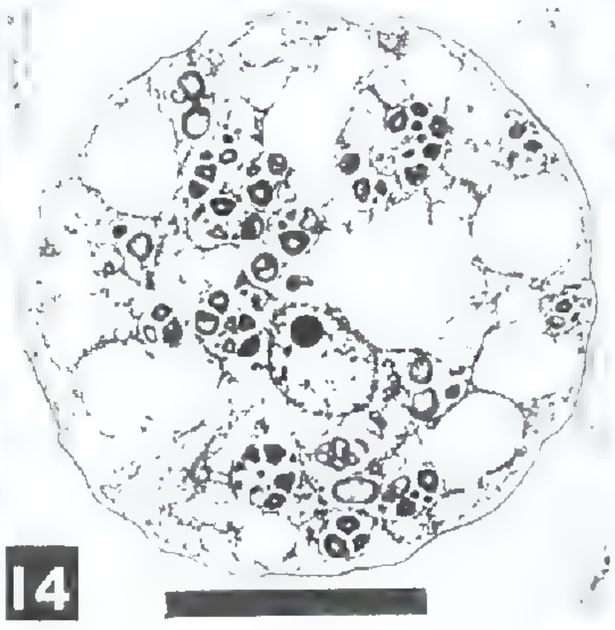
C. stagnalis

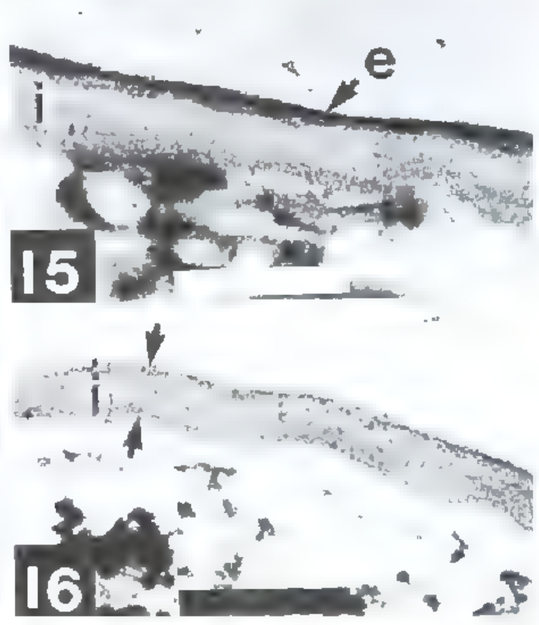
Callitriche stagnalis had pollen with a well-defined intectate exine that ranged from 0.50–0.95 μm in thickness (Figures 10–12). Distinct clavate and echinate elements characterized the sexine along with a thin, granular nexine (Figure 12). The nexine comprised approximately 17% of the total exine thickness. The structural elements were variably fused and arranged into a somewhat reticulate pattern (Figure 10). A dark-staining commissural line was present within the nexine, and underlaid by a layer of irregular relatively small granules (Figure 12).

C. hermaphroditica

Callitriche hermaphroditica had the most distinctive pollen wall structure of the species examined (Figures 13–16). Grains had a well-developed intine ranging from 0.25–0.45 μm in thickness (Figures 15 and 16). In contrast to the other species examined, the exine of *C. hermaphroditica* is best described as rudimentary. However, ultrastructural variability was evident, even among grains within the same anther. In plants of the perennial growth form (#2267), an exine wall component was virtually absent (Figure 16), while in the annual form (#2030) the exine formed a thin, homogeneous to granular band that was generally less than 0.1 μm in thickness (Figure 15). In other grains from the annual growth form, the exine element was manifested as small, irregularly shaped granules that ranged in size from 0.05–0.16 μm (not shown). The poorly developed exine in *C. hermaphroditica* is likely the cause for the irregular shape and smooth external appearance of the grains (Figure 13).







Figures 10–16. Scanning (Figures 10, 13) and transmission (Figures 11, 12, 14–16) electron micrographs of *Callitriche* pollen. Figures 10–12; *C. stagnalis*. **10.** View showing the interapertural region. Bar = 5 μm. **11.** Transverse section of an entire grain. Bar = 5 μm. **12.** Detail of transverse section of exine; note the thin nexine (n) and the thicker sculptured sexine. Bar = 1 μm. Figures 13–16; *C. hermaphroditica* (perennial form [#2267]: Figures 14 and 16; annual form [#2030]: Figures 13 and 15). **13.** View showing several nonacetolyzed grains; note the irregular shape. Bar = 10 μm. **14.** Transverse section of an entire grain; note the absence of a well-defined and darkly stained outer sporoderm layer (exine). Bar = 5 μm. **15.** Detail of transverse section of sporoderm; note the relatively thin, rudimentary exine (e) and the thicker underlying intine (i). Bar = 0.6 μm. **16.** Detail of transverse section of sporoderm showing the virtual absence of an exine component and relatively thick intine (i, between arrows). Bar = 0.6 μm.

DISCUSSION

This study confirms exineless pollen in *Callitriche*. The general pattern of a well developed exine in aerially flowering species and the virtual lack of an exine in the hypohydrophilous *Callitriche hermaphroditica* is demonstrated. However, exine thickness differed in annual (rudimentary) and perennial (absent) forms of this species. Martinsson (1993) reported reduction, but not absence, in numerous accessions of this species from Sweden. The significance of this infraspecific variation in exine thickness is not known, but may reflect the recent origin of hypohydrophily in *C. hermaphroditica* (see below, and Osborn and Philbrick, 1994).

There is also an apparent association between the growth habit (terrestrial versus amphibious) and the relative thickness of the basal layer. Pollen of the terrestrial species (*Callitriche peploides*) had a thicker nexine (30% of total exine) than any of the three amphibious species (10–20% of total exine). However, only a single terrestrial species was examined. Additional terrestrial species need to be examined before the significance of this apparent difference can be interpreted.

Although the lack (or extreme reduction) of an exine is closely correlated with hypohydrophily, the adaptive significance of this association is not understood. It is perhaps intuitive to predict that the loss of exine is a result of its release from selection pressures that maintain it. Yet, it is not known whether the exine is actually selected against during the evolution of hypohydrophily or is simply lost due to genetic drift. In general, the harmomegathic nature of the pollen exine is associated with controlling water relations of the grain during dispersal (desiccation) and hydration on the stigma (Heslop-Harrison, 1971). It is not clear whether this alone would translate into the loss of exine when such extremes in water potential are absent during hypohydrophilous pollination. On the other hand, there may be direct selective advantages associated with the lack of exine. Perhaps the pollen delivery system itself exerts selective pressures (e.g., Cox, 1988). Relationships among exine reduction and factors such as pollen-stigma interaction, emergence of the pollen tube, and pollen dispersal remain to be clarified in hypohydrophilous plants. It is also important to note that there are several examples of aerially flowering groups that have extremely reduced exines. The adaptive significance of exine reduction in these groups is also equivocal, but does not seem to be closely related to pollination systems (Kress, 1986).

Hypohydrophily is clearly a derived pollination system in angiosperms; the aerial floral biology is abandoned in favor of the release and capture of wet, water-borne pollen. In a functional sense hypohydrophily represents one of the most unique (divergent) forms of pollination in angiosperms. Because of the close relationship between floral form and pollination system function (e.g., Faegri and van der Pijl, 1979) it is intuitive to predict that the floral structure of hypohydrophilous species would reflect the functional divergence of the pollination system (i.e., be markedly different than related aerially flowering species). However, this

does not seem to be the case in *Callitriche* where relatively little modification in overall floral morphology is apparent. The degree of exine reduction in *C. hermaphroditica* contrasts markedly with the morphological similarity that otherwise characterizes the flowers, which may indicate that the strongest selective pressures that have operated during the evolution of hypohydrophily in *Callitriche* occur on pollen, not other floral characters.

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C. T. P.
DEPARTMENT OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES
WESTERN CONNECTICUT STATE UNIVERSITY
DANBURY, CONNECTICUT 06810

J. M. O.
DIVISION OF SCIENCE
NORTHEAST MISSOURI STATE UNIVERSITY
KIRKSVILLE, MISSOURI 63501

APPENDIX I

Collection information of specimens examined during this study. All voucher specimens are located in the herbarium of Western Connecticut State University. *C. heterophylla* var. *bolanderi*: WASHINGTON, Thurston Co., 22 June 1987, *Philbrick 2098*. *C. marginata*: CALIFORNIA, San Diego Co., 6 January, 1986, *Philbrick 1597*. *C. peploides*: ALABAMA, Conecuh Co., 14 March, 1988, *Philbrick and Haynes 2135*. *C. stagnalis*: WASHINGTON, Gray's Harbor Co., 20 June, 1987, *Philbrick 2096*. *C. hermaphroditica*: annual form—CALIFORNIA, Tuolumne Co., 31 May, 1987, *Philbrick 2030*; perennial form—CALIFORNIA, Shasta Co., 12 June, 1990, *Philbrick 2267*.

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NEW ENGLAND BOTANICAL CLUB

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The New England Botanical Club will offer an award of $1,000 in support of botanical research to be conducted by a graduate student in 1995. This award is made annually to stimulate and encourage botanical research on the New England flora, and to make possible visits to the New England region by those who would not otherwise be able to do so.

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The 1994 Graduate Student Research Award was presented to Andrea Stevens of the University of Massachusetts, in support of her work on the paleoecology of sandplain grasslands on Martha's Vineyard.

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CHROMOSOME COUNTS FOR *CALLITRICHE* (CALLITRICHACEAE) IN NORTH AMERICA

C. THOMAS PHILBRICK

ABSTRACT

Somatic chromosome numbers are reported for nine species and one variety of *Callitriche* (Callitrichaceae). The following new reports are included: $2n = 20$ (*C. nuttallii, C. marginata*), $2n = 40$ for one of four populations of *C. heterophylla* var. *heterophylla*, $2n = 40$ (*C. trochlearis*), $2n = 10$ (*C. peploides, C. terrestris*).

Key Words: *Callitriche*, chromosome numbers, North America

INTRODUCTION

Chromosome numbers vary considerably between species of *Callitriche* (Callitrichaceae), a family of ca. 50 species of largely temperate distribution. Diploid numbers range from $2n = 6$ to 40 (e.g., Schotsman, 1967; Philbrick, 1989). Yet, chromosome numbers are known for only approximately half of the species. The purpose of this contribution is to report on chromosome numbers of species of *Callitriche* that occur in North America. Herein, I report chromosome counts from 41 populations of the nine species and single variety that occur in this region.

MATERIALS AND METHODS

Chromosome counts were made from seedling root tips. Seeds were germinated on moist filter paper. Upon germination the seedlings were treated in 0.02% 8-hydroxyquinoline at 4°C for 2 hours and subsequently fixed in Carnoy's fixative (95% EtOH : chloroform : glacial acetic acid; 6:3:1) overnight at −5°C. After rinsing twice in distilled water, the root tips were hydrolyzed briefly in 1 N HCl and squashed in aceto-orcein. Counts were derived from a minimum of ten plants from each population. Voucher specimens are cited in Table 1. Voucher specimens are located at CONN.

RESULTS AND DISCUSSION

Chromosome counts were determined for 41 populations of the nine species and one variety of *Callitriche* in North America

Table 1. Chromosome number determinations for *Callitriche* in North America. All collections are by Philbrick unless otherwise noted.

C. hermaphroditica L. *2n* = 6. CANADA. **Alberta**. Edmonton, September 1985, *1609*. **British Columbia**. Merritt, 28 August 1988, *2157*. **Quebec**. Portneuf Co.: St. Augustin, 2 September 1988, *Philbrick & Bruneau 2166*. U.S.A. **California**. Madera Co.: 30 May 1987, *2022*; Tuolumne Co.: 31 May 1987, *2033*.

C. heterophylla var. *heterophylla* Pursh. *2n* = 20. U.S.A. **Mississippi**. Lowndes Co.: 15 March 1988, *Philbrick & Haynes 2144*. **New York**. St. Lawrence Co.: 19 September 1987, *Philbrick & Gale 2112*. **New Hampshire**. Rockingham Co.: 20 August 1990, *2112*. *2n* = *40*. **New Hampshire.** Carroll Co.: 29 November 1992, *Philbrick, Philbrick & Philbrick 3192*.

var. *bolanderi* (Hegelm.) Fassett. *2n* = 20. CANADA. **British Columbia**. Vancouver Island, 8 June 1988, *2155*. U.S.A. **California**. Madera Co.: 30 May 1987, *2021*; Humboldt Co.: 9 June 1987, *2046*; Riverside Co.: 22 May 1987, *2002*. **Washington**. Jefferson Co.: 20 June 1987, *Philbrick, Busse & Philbrick 2088*.

C. marginata Torrey. *2n* = 20. CANADA. **British Columbia**. Vancouver Island, 7 June 1988, *Philbrick, Ceska, Ceska & Catling 2156*. U.S.A. **California**. San Diego Co.: 6 January 1986, *1598*; Marin Co.: 5 June 1987, *Philbrick & Rubtzoff 2040*; Solano Co.: 2 June 1987, *Philbrick & Anderson 2035*.

C. nuttallii Torrey. *2n* = 20. U.S.A.. **Alabama**. Conecuh Co.: 14 March 1988, *Philbrick & Haynes 2136*; Butler Co.: 14 March 1988, *Philbrick & Haynes 2137*; Lowndes Co.: 14 March 1988, *Philbrick & Haynes 2139*; Pickens Co.: 15 March 1988, *Philbrick & Haynes 2142*. **Mississippi**. Kemper Co.: 15 March 1988, *Philbrick & Haynes 2147*.

C. peploides Nutt. *2n* = 10. U.S.A. **Alabama**. Mobile Co.: 13 March 1988, *Philbrick & Haynes 2127*; Escambia Co.: 13 March 1988, *Philbrick & Haynes 2131*; Conecuh Co.: 14 March 1988, *Philbrick & Haynes 2135*; Lowndes Co.: 14 March 1988, *Philbrick & Haynes 2140*.

C. stagnalis Scop. *2n* = 10. U.S.A. **Maryland**. St. Mary's Co.: 30 September 1984, *1386*. **Oregon**. Jackson Co.: 11 June 1987, *2053*; Clackamas Co.: 13 June 1987, *2067*; Pacific Co.: 16 June 1987, *2083*. **Washington.** Grays Harbor Co.: 22 June 1987, *2102*.

C. terrestris Raf. *2n* = 10. U.S.A. **Mississippi**. Kemper Co.: 15 March 1988, *Philbrick, Haynes & McDaniels 2145*; Lowndes Co.: 15 March 1988, *Philbrick, Haynes & McDaniels 2145*. **Tennessee**. Dickson Co.: 29 April 1985, *1403*; Benton Co.: 29 April 1985, *1404*.

C. trochlearis Fassett. *2n* = 40. U.S.A. **California**. Mendocino Co.: 8 June 1987, *2043*. **Oregon**. Coos Co.: 11 June 1987, *2057*.

C. verna L. *2n* = 20. CANADA. **Quebec**. Portneuf Co.: St. Augustin, 2 September 1988, *Philbrick & Bruneau 2167*; Charlevoix Co.: 2 September 1988, *Philbrick & Bruneau 2168*. U.S.A. **California**. Sonoma Co.: 7 June 1987, *2041*. **Colorado**. Larimer Co.: 4 August 1984, *3121*. **New Hampshire**. Coos Co.: 4 September 1988, *2176*.

north of Mexico. Counts for three species confirm those that have previously been published: $2n = 20$ for *C. heterophylla* var. *heterophylla* Pursh (e.g., Loeve and Kapoor, 1967; Taylor and Mulligan, 1968) and *C. heterophylla* var. *bolanderi* (Hegelm.) Fassett (e.g., Taylor and Mulligan, 1968), and $2n = 6$ for *C. hermaphroditica* L. (e.g., Love, 1982; Schotsman, 1967). It is notable that a single population of *C. heterophylla* var. *heterophylla* exhibited $2n = 40$ instead of the typical $2n = 20$. This is the first report of an octoploid population of this species, but it is yet unclear if it is of alloploid or autoploid derivation. The count for *C. stagnalis*, which is introduced from Europe (Fassett, 1951), is the same as reported from European populations (e.g., Schotsman and Andreas, 1980).

Prior to this study chromosome counts were unknown for five species of *Callitriche* in North America. Thus, the counts provided herein are the first for these species ($2n = 20$ for *C. marginata* Torrey and *C. nuttallii* Torrey, $2n = 10$ for *C. peploides* Nutt. and *C. terrestris* Raf., and $2n = 40$ for *C. trochlearis*).

The chromosome counts reported herein parallel the range in numbers in the genus worldwide (Philbrick, 1989). Based on $x = 5$ there are two phyletic chromosome number series in *Callitriche*: the euploid series ($2n = 10, 20, 40$) and aneuploid reduction series ($2n = 8, 6$). All the species in North American belong to the euploid series with the exception of *C. hermaphroditica* ($2n = 6$).

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DEPARTMENT OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES
WESTERN CONNECTICUT STATE UNIVERSITY
DANBURY, CONNECTICUT 06810

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